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CARACTÉRISATION DE LA MACROFAUNE ÉPIBENTHIQUE DE L'ESTUAIRE ET DU NORD DU GOLFE DU SAINT-LAURENT (QUÉBEC-CANADA) EN RELATION AVEC LES PARAMÈTRES ENVIRONNEMENTAUX : ANALYSES MULTIVARIÉES ET APPROCHE DE GÉOSTATISTIQUE

MÉMOIRE

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RÉSUMÉ

La société actuelle est confrontée à divers problèmes environnementaux d'envergure tels que le réchauffement climatique et la perte de biodiversité. La moindre modification de l'environnement peut avoir des conséquences graves sur les habitats et les ressources. L'étude de la structure des communautés benthiques et des poissons commerciaux du Saint-Laurent permet de détecter des perturbations potentielles. En 2006, le relevé annuel multidisciplinaire de chalutage de fond, effectué par le ministère des Pêches et des Océans du Canada, a permis de recueillir des informations sur l'ensemble de la faune macrobenthique de l'Estuaire et du nord du Golfe du Saint-Laurent.

Notre objectif principal était de caractériser la macrofaune benthique de la zone d'étude. Pour y parvenir, la distribution spatiale des communautés a d'abord été explorée via l'emploi d'analyses multivariées (nMDS). Ainsi, à l'étude des assemblages et de l'analyse visuelle de la carte de diversité benthique de la région, l'Estuaire et le nord du Golfe ont pu être divisés en huit régions biogéographiques distinctes. Des analyses canoniques ont par la suite été appliquées afin de tester les corrélations existantes entre les données d'abondance d'espèces et les variables environnementales présentes dans le milieu. Globalement, la concentration en oxygène dissout, la température, la profondeur, la valeur maximale des courants de fond ainsi que la présence de pelite et de gravier dans les sédiments, sont les paramètres retenus. Par ailleurs, nous avons pu constater que la réponse de trois taxons d'invertébrés diffère grandement face au phénomène d'hypoxie identifié dans l'Estuaire, résultant en une densité plus élevée des organismes tolérants tels que les cnidaires et les mollusques, contrairement aux crustacés. Les analyses de cette étude ont été conclues par une modélisation d'habitat, basée sur les modèles linéaires généralisés (GLM), dans le but de prédire les habitats potentiels des communautés en fonction des paramètres environnementaux étudiés. L'équation résultante de la modélisation a ainsi retenu une combinaison de variables, soit : l'oxygène dissout, la profondeur, la température et le courant de fond. Qui plus est, près de 40 % de la variation des données biologiques est ainsi expliquée par l'équation résultante. La carte de prédiction d'habitats potentiels, comportant des similarités frappantes avec la carte de diversité établie suite au relevé, expose de ce fait des zones à grand potentiel de conservation benthique près de la région de la Minganie, de la fosse de Mécatina, du détroit de Belle-Isle et sur la côte ouest terre-neuvienne.

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INTRODUCTION GÉNÉRALE

Depuis quelques années, l'exploitation excessive des ressources par l'homme a eu comme conséquence la perte de biodiversité (Worm *et al.*, 2006). Ainsi, le nombre de recherches axées vers l'analyse des impacts du changement de biodiversité sur les écosystèmes a considérablement augmenté avec les années. L'exploitation des ressources par la société de consommation induit, en effet, des modifications considérables sur l'écosystème. À titre d'exemple, afin d'assurer sa pérennité et d'améliorer son bien-être quotidien, les diverses actions entreprises par l'homme ont pour conséquence de fragmenter l'habitat des forêts et des prairies (Thompson Hobbles *et al.*, 2008). L'eutrophisation des cours d'eaux est également le résultat d'actions anthropiques telles que le développement d'infrastructures en milieu côtier et l'utilisation de certaines technologies agricoles (Tilman *et al.*, 2001). L'écosystème marin, quant à lui, est exposé aux éventuels impacts des changements climatiques (Kerr, 2007; Wang et Overgaard, 2007). Il est également vulnérable aux perturbations causées par la pêche commerciale, telle que la modification potentielle de l'habitat de la faune benthique (Jennings et Kaiser, 1998; Auster et Langton, 1999). Plusieurs aspects de la relation entre la biodiversité et le fonctionnement des écosystèmes restent à identifier ou à confirmer. Par contre, un consensus au sein de la communauté scientifique démontre que les systèmes les plus diversifiés sont également les plus performants. En d'autre termes, plus la diversité est élevée, moins les chances d'introduction d'espèces exotiques envahissantes sont grandes (Loreau *et al.*, 2001). Qui plus est, la diversité élargit les possibilités de réponses des espèces face à une perturbation

du milieu, résultant en une augmentation de la stabilité de l'écosystème (Hooper *et al.*, 2005). Le développement d'outils afin de déterminer le niveau de biodiversité des écosystèmes, d'évaluer la vulnérabilité des régions et de mesurer les changements de biodiversité, est ainsi devenu nécessaire afin d'élaborer des mesures de conservation adéquates.

Plus de 65 % de la surface de la terre est recouverte d'eau. Ainsi les organismes résidant en ces fonds marins constituent le plus grand groupe faunique de la Terre (Snelgrove, 1998). Toutefois, bon nombre de connaissances sur ces organismes restent à découvrir. À l'échelle planétaire, près de 1,75 millions d'espèces seraient répertoriées, ce qui représente en soit une proportion minime par rapport à la quantité globale estimée, avoisinant les 3,6 à plus de 100 millions d'espèces (UNEP-World Conservation Monitoring Center). Qui plus est, les efforts de conservation de la biodiversité semblent être beaucoup plus axés au niveau terrestre que marin. À titre d'exemple, un texte de 600 pages traitant de la conservation biologique (Meffe et Carroll, 1994), ne contient que deux pages portant sur la biodiversité marine.

Quant aux océans, il y aurait, selon Grassle et Maciolek (1992), entre 1 et 10 millions d'espèces vivantes. Considérant que les écosystèmes marins fournissent un nombre considérable de produits et de services essentiels (ex : poissons, fruits de mer, sel, moyen de transport), il est d'autant plus important d'améliorer les connaissances sur la

biodiversité des organismes qui s'y retrouvent. Comme le mentionnent Rosenberg *et al.* (2004), les organismes benthiques représentent une faune vulnérable aux impacts écologiques ainsi qu'à tous les types de pollution produits, qui finissent tôt ou tard, par se déposer sur le fond marin. C'est donc pourquoi la faune benthique est très utilisée à titre d'indicateur de stress naturel ou anthropogénique encouru par l'écosystème (Borja *et al.*, 2000 ; Rosenberg *et al.*, 2004).

Depuis plusieurs années, bon nombre d'études dénotent l'importance de considérer les variables environnementales à titre de forces structurantes sur la distribution des communautés benthiques (Rosenberg, 1995 ; Freeman et Rogers, 2003). Comme le mentionnent Glockzin et Zettler (2008), deux étapes distinctes sont importantes afin de comprendre les patrons écologiques de la macrofaune. Cela consiste d'abord en la description des patrons de distribution des organismes, suivie de la détermination des paramètres qui influencent ces distributions spatiales. La caractéristique sédimentaire est très souvent suggérée comme l'une des variables capitales influençant la distribution des communautés benthiques (Rhoads et Germano, 1986; Sciderer et Newell, 1999; Kostylev *et al.*, 2001 ; Savicente-Anorve *et al.*, 2002). Dans cette même optique, il faudrait considérer les facteurs physiques qui peuvent agir et structurer ce substrat de fond tels que le régime hydrodynamique et la variation de la topographie. À ce propos, Rosenberg (1995) affirme que l'énergie physique présente près du fond marin représente un facteur déterminant sur la distribution spatiale des différents types de sédiments. Dans le contexte de réchauffement climatique actuel, la température est également un facteur environnemental primordial à

considérer en tant que force structurante sur les communautés benthiques. De plus, un certain nombre de recherches dénotent l'impact considérable d'une diminution d'oxygène sur les organismes de fond (Pihl *et al.*, 1992 ; Keister *et al.*, 2000 ; Wu, 2002 ; Diaz et Rosenberg, 2008), ce qui constitue donc un autre paramètre abiotique auquel il faut porter attention.

Avec les années, plusieurs travaux ont exposé les impacts des changements drastiques de la concentration en oxygène dissout retrouvée près des fonds en milieu marin (Diaz et Rosenberg, 1995; Rabalais *et al.*, 2001; Gilbert *et al.*, 2005). Un environnement est qualifié hypoxique lorsque la concentration en oxygène dissout se retrouve sous le seuil de 2 mgO_2/L ou 62,5 µmol/L (Diaz et Rosenberg, 1995). Par contre, ce seuil ne fait pas l'unanimité pour l'ensemble de la faune marine puisque pour certains organismes le seuil hypoxique se situe à une concentration plus élevée que celui de 2 mgO_2/L (Vargo et Sastry, 1977). Par ailleurs d'autres travaux concluaient que le nombre de régions touchées de façon permanente ou saisonnière par le phénomène d'hypoxie avait augmenté (Diaz et Rosenberg, 2008). Suite à l'examen des seuils de tolérance des différents taxons de la faune marine, un large éventail des conséquences associées à l'hypoxie a été mis en évidence (Vaquer-Sunyer et Duarte, 2008). Ce phénomène peut diminuer, voire éliminer, les espèces sensibles retrouvées en ces lieux hypoxiques, ce qui a donc pour conséquence de changer la composition des invertébrés benthiques (Bourque, 2008), des poissons ainsi que des communautés planctoniques (Wu, 2002). Globalement, l'hypoxie tend à diminuer la richesse spécifique du milieu. Des données historiques sur les conditions

environnementales retrouvées dans la couche profonde de l'Estuaire du Saint-Laurent, au Canada, ont démontré une diminution importante de la concentration en oxygène pour la période 1930-2003 (Gilbert *et al.*, 2005). Les valeurs enregistrées indiquent une chute de plus de 50 % de la quantité d'oxygène disponible, passant d'une concentration en oxygène dissout de 125 µmol/L à 60 µmol/L en 70 ans. Cependant, nos connaissances sur l'impact et l'évolution du phénomène d'hypoxie dans les eaux profondes du Saint-Laurent ne sont encore que fragmentaires. Des recherches plus approfondies doivent entre autre être effectuées dans le but de définir les conséquences de la diminution de l'oxygène dissout sur les habitats benthiques.

Avec la conscientisation du phénomène de réchauffement climatique et des défis de tailles auxquels seront confrontés les écosystèmes, la température est devenue une variable cruciale à considérer dans les études de caractérisation d'habitat faunique telle que la présente étude. D'autre part, sachant que le taux métabolique des invertébrés benthiques est principalement influencé par la température (Peters, 1983), toute augmentation au niveau de ce paramètre environnemental pourrait avoir des effets considérables sur les organismes et leur distribution. La modification des paramètres environnementaux tels que les courants de fond, la stratification de la colonne d'eau, la production primaire ou la température peut influencer les fonctions physiologiques des organismes présents (Danovaro *et al.*, 2007). D'ailleurs, il existe plusieurs travaux investigant les stratégies de reproduction des organismes adultes et du développement larvaire qui s'ensuit, en relation avec les variables environnementales qui prévalent dans le milieu (Morgan et Christy, 1994; McEdward,

1997). Deux variables influencent principalement la durée et la survie des larves planctoniques, soit la nourriture et la température (Reitzel *et al.*, 2004). Par conséquent, que ce soit directement ou indirectement, la température peut influencer significativement la structure des communautés d'invertébrés benthiques.

L'écosystème du Saint-Laurent, situé à l'est du Canada, est un exemple parfait de système productif constitué d'une grande gamme de conditions océanographiques distinctes (Roy *et al.*, 2000). Le Golfe du Saint-Laurent est très souvent divisé en sous-régions biogéographiques, basées principalement sur les caractéristiques océanographiques et les conditions physico-chimiques retrouvées dans chacune d'elles. Koutitonsky et Bugden (1991) proposent d'ailleurs une division en huit sous-régions, principalement classifiées en fonction des conditions physiques du milieu. De leur côté, Brunel *et al.* (1998) proposent vingt zones basées sur le contour côtier et des critères océanographiques, biogéographiques et bathymétriques. C'est pourquoi le système hétérogène que représente le Saint-Laurent, constitue une zone d'étude par excellence afin d'évaluer les relations potentielles entre les communautés benthiques et les facteurs environnementaux du milieu.

Jusqu'à ce jour, plusieurs études ont tenté de décrire la diversité et la distribution des communautés d'invertébrés benthiques dans l'Estuaire et le nord du Golfe du Saint-Laurent (EGSL). Bon nombre d'entre elles se sont orientées vers un taxon précis plutôt que sur l'ensemble de la communauté présente. À titre d'exemple, une étude sur les mollusques

a été exposée par Robert (1979), et une autre a été décrite sur les polychètes par Massad et Brunel (1979). Par ailleurs, des recherches quantitatives sur la faune endobenthique ont également été effectuées (Préfontaine et Brunel, 1962 ; Peer, 1963 ; Ouellet, 1982). Récemment, des investigations sur les assemblages de l'endofaune ont été menées en lien avec les traces de bioturbation retrouvées (Belley *et al.*, 2008), ainsi qu'en relation avec les facteurs environnementaux de l'EGSL (Desrosiers *et al.*, 2000; Bourque, 2008). Malgré cela, la faune d'invertébrés benthiques demeure encore peu connue.

En août 2006, l'échantillonnage approfondi de la macrofaune épibenthique a été incorporé au relevé multidiciplinaire annuel du nord du Golfe du Saint-Laurent, effectué par le ministère des Pêches et des Océans du Canada. Exécutée avec l'aide d'un chalut démersal, cette mission représentait une tout première en termes d'étude à grande échelle, jumelant la cueillette de données d'abondance de la faune benthique (commerciale et non-commerciale) et des variables environnementales du milieu. Bien que cet instrument de pêche ne soit pas le plus adéquat et le plus précis possible pour échantillonner la macrofaune benthique, les résultats obtenus se sont avérés à la hauteur de nos espérances afin de caractériser cette faune sur un aussi grand territoire d'étude. L'utilisation du nouveau chalut de type *Campelen 1800* permet effectivement de recueillir un plus grand nombre d'espèces benthiques que son prédécesseur (*URI 81'/114'*). À titre d'exemple, *Brisaster fragilis*, *Ctenodiscus crispatus* et plusieurs autres espèces d'anémones ont vu leur proportion passer de nulle jusqu'à un pourcentage maximal de 62 % d'occupation dans le chalut (comm. perso. C. Savenkoff). Nul doute que cette mission à donc permis de

recueillir un nombre considérable de connaissances pour la gestion durable et pour les initiatives de protection ou de conservation à venir.

L'un des défis actuels dans la gestion des écosystèmes marins est de déterminer les zones prioritaires à protéger. Pour y arriver, les zones à grande diversité, ainsi que les régions habitées par des espèces rares et menacées, doivent être identifiées. L'une des stratégies disponibles est de créer une carte continue de prédiction d'habitat potentiel qui dicte la présence de communautés d'espèces, en fonction de l'habitat physique optimal à ces derniers (Degraer *et al.*, 2008). Une fois le modèle de prédiction établi, il devient plus facile de mettre à jour ces données de distribution spatiale en fonction des variables environnementales disponibles. Ainsi, en ayant une carte contenant l'ensemble des paramètres environnementaux présents dans la zone d'étude, il est par la suite possible de créer une carte continue de prédiction de la distribution spatiale de la macrofaune benthique (Degraer *et al.*, 2008). Qui plus est, ce genre de modèle considère l'état dynamique des communautés spécifiques répondant aux changements environnementaux. De plus, la prédiction d'habitat est une approche qui peut déterminer les conséquences possibles des changements environnementaux sur la distribution des espèces (Woodward et Cramer, 1996; Vaz *et al.*, 2004 ; Martin *et al.*, 2005).

Les objectifs de la présente étude sont donc d'utiliser les échantillons recueillis lors de la mission multispécifique réalisé à l'été 2006 afin : (1) d'explorer la structure, la

composition et la distribution des espèces de la macrofaune benthique à l'aide d'analyses multivariées ; (2) de relier la distribution spatiale des espèces avec les facteurs abiotiques, dans le but de déterminer lesquels de ces paramètres environnementaux expliquent le plus les patrons d'espèces ; (3) d'évaluer l'influence de la diminution de l'oxygène dissout dans la partie profonde de l'Estuaire maritime du Saint-Laurent, sur la variabilité spatiale des organismes benthiques, et ; (4) d'utiliser les techniques de géostatistiques et de cartographie (ArcGIS) afin de décrire les affinités des communautés de la macrofaune avec les variables environnementales significatives, résultant en un modèle de prédiction d'habitat potentiel. Plus spécifiquement, les hypothèses supposent que les distributions spatiales des assemblages de communautés benthiques, de même que la diversité, seront influencées par la température et la concentration en oxygène dissout. Ces deux paramètres environnementaux devraient ainsi être utilisés afin de prédire la distribution de la macrofaune benthique dans la modélisation d'habitat.

Ce mémoire de maîtrise, sous forme d'article scientifique, est rédigé en anglais et contient un chapitre. Cet article devrait être prochainement soumis à la revue *ICES Journal of Marine Science*.

CHAPITRE I

EPIBENTHIC MACROFAUNA COMMUNITY STRUCTURE OF THE NORTHERN GULF OF ST. LAWRENCE IN RELATION TO ENVIRONMENTAL FACTORS: MULTIVARIATE AND GEOSTATISTICAL APPROACHES

1.1 Introduction

In the last decade, the increase of natural resources exploitation by human resulted in biodiversity losses (Worm *et al.*, 2006). Motivated by the decline of biodiversity, large number of researches focuses on the effect of biodiversity losses or changes on ecosystem structure and functioning. Marine ecosystems are vulnerable to direct disturbance through fishing such as the modification of benthic habitat fauna (Jennings and Kaiser, 1998; Auster and Langton, 1999). They are also exposed to potential impact of climate change (Kerr, 2007; Wang and Overgaard, 2007). Many aspects of the relationship between biodiversity and ecosystem functioning remain to be confirmed but for some results, consensus was found in the scientist community. An increasing in species richness will generally decrease the possibility of an invasion of exotic species (Loreau *et al.*, 2001). Moreover, species diversity gives a wide range of responses to the different environmental perturbations helping then to stabilize the ecosystem (Hooper *et al.*, 2005). The development of tools to determine the biodiversity level, to estimate the vulnerability of specific regions and to monitor the biodiversity changes is a necessity to elaborate conservation measures.

As the world surface is covered by more than 65% of deep-sea sediment, the organisms residing on and in the seabed are the largest faunal assemblages on Earth (Snelgrove, 1998). Futhermore, many areas are unexplored and limited knowledge of these areas constitutes a major hurdle to management practices to conserve marine resources. Considering that marine ecosystems provide a large number of essential

services to human, such as fishes, seafoods and mean of transportation, it is therefore important to improve our understanding of the biodiversity of these marine benthic organisms.

Numerous benthic ecology studies had already proved the importance of environmental factors as driving forces on benthic community distribution (Rosenberg, 1995; Freeman and Rogers, 2003; Bourque, 2008). As suggested by Glockzin and Zettler (2008), to understand the ecological patterns of macrofauna, it requires two-stages procedure: (1) the description of the patterns in the distribution of the organisms and; (2) the determination of the parameters causing this distribution. The sedimentary characteristic is often suggested as one of the main factors influencing the structure of the marine benthic community distribution (Rhoads and Germano, 1986; Seiderer and Newell, 1999; Kostylev *et al.*, 2001; Savicente-Anorve *et al.*, 2002). Moreover, we also have to consider the physical factors inducing changes to the substratum composition such as hydrodynamic processes and topographic variation. In fact Rosenberg (1995) suggested that physical energy above the seabed is an important factor for the spatial distribution of the different sediment types. In a global warming context, temperature should also be studied as a driving factor on benthic communities. Moreover, the impact of oxygen depletion on invertebrates was also addressed in many studies as a significant abiotic factor (Pihl *et al.*, 1992; Keister *et al.*, 2000; Wu, 2002; Diaz and Rosenberg, 2008).

There are indications that lead to believe that climatic changes can affect marine ecosystem. Temperature variations can influence metabolic rates of organisms and other environmental factors such as local currents, water column stratification, nutrient cycling and primary production (McGowan *et al.*, 1998). These variables can strongly affect the dynamic of the marine community and over the time, the physiological function of the organisms (Danovaro *et al.*, 2007). Thus, all these processes, directly or indirectly affected by temperature, may cause differences in the benthic invertebrate community structure.

Over the years, many results showed about the impact of drastic changes of dissolved oxygen level in bottom water on marine organisms (Diaz and Rosenberg, 1995; Rabalais *et al.*, 2001). Most reports proposed a threshold value of 2 mgO_2/L (62.5 µmol/L) or lower to qualify an hypoxic environment (Diaz and Rosenberg, 1995). Nevertheless, this threshold value can be inadequate for many organisms for which hypoxia impacts are encountered at higher oxygen concentrations (Vargo and Sastry, 1977). Although the number of areas with hypoxia episode increased in number over the world (Diaz and Rosenberg, 2008), consequences of hypoxia on marine life are variable, considering oxygen thresholds among taxa (Vaquer-Sunyer and Duarte, 2008). Hypoxia can eliminate sensitive species, thereby causing major changes in species composition of benthic invertebrates (Bourque, 2008), fish and phytoplankton communities (Wu, 2002). Globally, hypoxia results in a general decrease in the species richness. Historical data for oxygen concentrations in the deep layer of the Lower St. Lawrence Estuary (LSLE), Eastern Canada, indicated an important decline for the 1930-2003 period (Gilbert *et al.*,

2005). The recorded oxygen values indicate a drop-off of more than 50%, from 125 µmol/L to 60 µmol/L in 70 years.

The St. Lawrence system is a productive marginal area with a large range of oceanographic conditions (Roy *et al.*, 2000). With the variety of hydrodynamic regimes and physical parameters observed, the Gulf of St. Lawrence (GSL) is often divided into sub-regions based on knowledges about oceanographic characteristics. Koutitonsky and Bugden (1991) proposed eight sub-regions mainly classified on the basis of physical conditions: Brunel *et al.* (1998) proposed 20 marine zones, classified on the basis of coastal contour, oceanographic, biogeographic and bathymetric criteria. So, this heterogeneous system is a perfect study area to evaluate the potential link between benthic communities and environmental factors.

For the Estuary and the northern Gulf of St. Lawrence (EGSL), many studies described diversity and distribution of benthic invertebrate communities. Most studies focussed on specific taxa such as molluscs (Robert, 1979) and polychaetes (Massad and Brunel, 1979). Few studies investigated the infauna over the years with a quantitative approach (Préfontaine and Brunel, 1962; Peer; 1963; Ouellet, 1982; Bourque, 2008). Recently, investigations on the infauna assemblages and bioturbation traces (Belley *et al.*, 2008) in relation with environmental factors were conducted in the Estuary and the Gulf of St. Lawrence (Desrosiers *et al.*, 2000; Bourque, 2008). Nevertheless, the benthic invertebrate fauna of the St. Lawrence system are still poorly known.

In August 2006, monitoring of epibenthic invertebrate macrofauna was implanted during the annual summer groundfish survey of the northern Gulf of St. Lawrence performed by the Canadian Department of Fisheries and Oceans (DFO). This kind of study represented the first one over a wide geographical area including both benthic invertebrate species (commercial and non-commercial) abundances and environmental data in the St. Lawrence system. This is the first attempt to characterize quantitatively the benthic habitat over the whole EGSL system.

Several definitions existed to define the term habitat. According to Baretta-Bekker *et al.* (1992), habitat can be simply defined as the characteristic space occupied by population or a species. Using a similar approach method than the present study, CHARM's team (Eastern Channel Habitat Atlas for Marine Resource Management) defined habitat as an area with specific environmental conditions in which organism, population or community can survive (Carpentier *et al.*, 2005). In fact, in the environment, most communities appear to occur within a recognizable suite of physical conditions, whereas other ones occur within a more tightly defined physical habitat than other (Urbanski and Szymelfenig, 2003). Thus, the habitat suitability (HS) model highlights the close relationship between the physical environment of the study area and the biological composition of its associated community (Guisan and Zimmerman, 2000; Hirzel and Arlettaz, 2003; Hirzel *et al.*, 2006; Degraer *et al.*, 2008).

The actual challenge is to identify the potential protect areas that will contribute to the conservation of the biodiversity. One of the strategies is to create a full coverage mapping tool rather than a map with simply punctual data restricted to observation points. Resulting in HS model, it predicts the presence of benthic invertebrate community based on the suitability of the physical habitat (Degraer *et al.*, 2008). As Degraer *et al.* (2008) mentioned, if full coverage maps of the environmental variables are available, it is possible to create a full coverage map of the macrobenthos spatial distribution. Besides, very few ecological studies considered the dynamic state of community species in response to environmental changes. The HS model is a truly dynamic approach to study the possible consequences of a changing environment on species distribution (Woodward and Cramer, 1996). Thus, predicting species or communities occurrence using this modelling approach have become increasingly common in ecological conservation study such as in entomology (Hein *et al.*, 2007), mammalogy (Catullo *et al.*, 2008) and oceanography (Vaz *et al.*, 2004; Martin *et al.*, 2005; Degraer *et al.*, 2008).

The objectives of this study are to: (1) explore with multivariate analyses the structure, composition and distribution of the epibenthic macrofauna species; (2) correlate the spatial distribution with the abiotic factors and to determine which environmental parameters explain the best species pattern; (3) evaluate the influence of hypoxic area in the Lower Estuary on spatial distribution of benthic organisms by using mapping approach and; (4) use geostatistic and generalized linear model to describe the macrofauna community affinity with significant environmental parameters, resulting at

HS model. The result of this study will help scientists and decision-makers to develop guidelines priorities for adequate conservation measures of benthic habitats.

1.2 Material and methods

1.2.1 Study area

The Gulf of St. Lawrence (GSL) is a highly stratified semi-enclosed sea with an approximate basin surface area of 226 000 km^2 (Koutitonsky and Bugden, 1991). The Gulf has two major connections with the Atlantic Ocean, through the Cabot and the Belle Isle straits, and receives important freshwater inflows from the St. Lawrence River and other tributaries. Consequently, estuarine circulation is created with water flowing seaward in the surface layer and landward in the deep layer (Saucier *et al.*, 2003). The topography of the Gulf is distinguished by three channels (Laurentian, Anticosti and Esquiman) (Fig. 1). The Laurentian channel is the deepest one with an average depth of 420 m, extending from the Cabot Strait to the mouth of Saguenay fjord in the Lower St. Lawrence Estuary. In contrast, a large and shallow area (average depth 50 m) known as the Magdalen shallow is found in the southwestern part of the Gulf (Dickie and Trites, 1983). A wide range of hydrodynamic conditions are found in this semi-enclosed sea, such gyres, seasonal variation in vertical stratification, fronts and seasonal ice cover (Therriault, 1991). These distinct hydrodynamic and topographic characters cover a broad range, which suggests that the Gulf can not be considered as an homogeneous system. As suggested by Rosenberg (1995) and Freeman and Rogers (2003), it is important to take

into account the variability of environmental parameters in marine ecology study, because it can influence the distribution and behaviour of marine organisms.

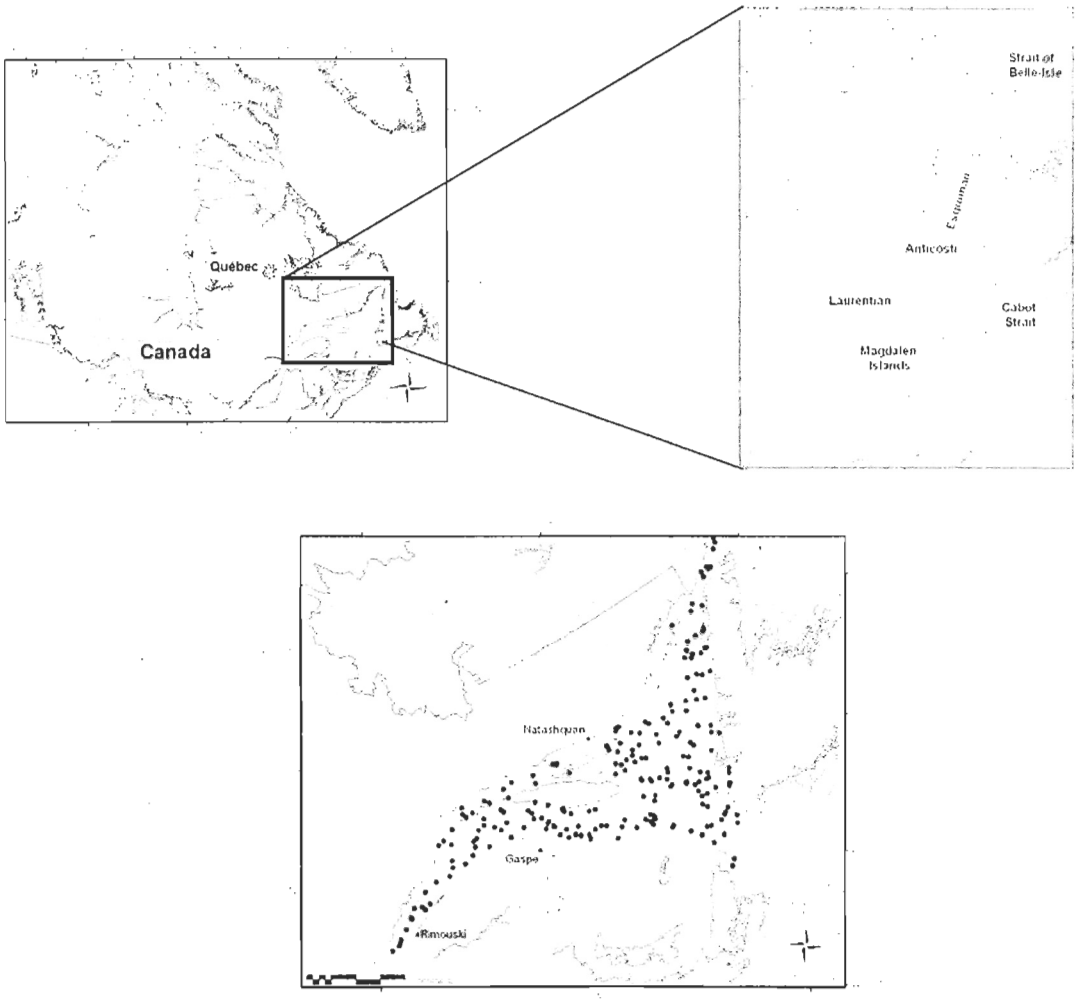

Figure 1. Study area showing the location of the 193 sampling stations of macrofauna, in August 2006.

1.2.2 Sampling gear and protocol

Macrofauna were collected from 193 stations in the Estuary and the northern Gulf of St. Lawrence (EGSL) during the annual summer groundfish survey made by the Canadian Department of Fisheries and Oceans (Quebec Region), aboard the CCGS *Teleost* research trawler from August 1st to 31 st, 2006. The sampling strategy used consisted of a stratified random sampling following predetermined strata based on depth (Doubleday, 1981)

Samples were collected with a four–sided shrimp bottom trawl (*Campelen 1800* type). It was rigged with variable net mesh sizes appropriate for each part of the trawl: 80 mm ("center knot" to "center knot") for the wings, 60 mm for the first belly and the square, and 44 mm for the second and third bellies. The codend and the lengthening piece are also 44 mm stretched mesh size and are equipped with a 12.7 mm knotless nylon lining. Trawl is fitted with a Rockhopper footgear (McCallum and Walsh, 2002) (Appendix 1). The standard tow duration was 15 minutes on the bottom, being shorter depending on the roughness of the substrata. Scanmar™ hydroacoustic sensors monitor trawl characteristics configuration (e.g. distance between doors and wings, vertical net opening and bottom depth).

Fish and invertebrates were sorted, identified, counted, and weighed. All were identified to the lowest taxonomic level possible for which identification is certain (see

list Appendix 2). Invertebrate species that were not easily identifiable were preserved in 70% ethanol or frozen for later identification in laboratory. Taxonomic names were verified on the Integrated Taxonomic Information System online (www.ITIS.gov). Density estimates for all identified macrofauna taxa were obtained by dividing the number or mass by the total area swept by the trawl, which defines the effort. Catch per unit effort (CPUE) was used as standardized abundance indices. Biomass density indices in kg/km^2 were used for many taxa that were too abundant to be counted. Colonial organisms such as Bryozoa and Hydrozoa could not be enumerated and were expressed in kg/km^2 in the database. The taxa Cnidaria and Echinodermata, predominantly composed of *Brisaster fragilis*, *Ctenodisicus crispatus*, *Gorgonocephalus* sp. and *Strongylocentrotus* sp., were also included in this database. The other taxa were expressed as ind/km^2 (abundance database). This, result in two different databases; one expressed as biomass and the other one expressed in abundance, these two databases do not consider the same species. However a third one using occurrence (P/A) data contained all the surveyed species.

1.2.3 Environmental data

A CTD Seabird™ apparatus (SBE911 Plus), equipped with five sensors, were used to measure depth and water characteristics of the water column such as conductivity, oxygen, temperature and concentration in chlorophyll *a*, closed to the sampling stations. Titrations of water samples were done to corroborate the concentration of dissolved oxygen at predetermined depths. Chlorophyll *a* data were calculated in laboratory in

using a specific standard curve for each Gulf sub-region (S. Plourde, pers. comm.). A digital map of seabed sediment types, originating from Loring and Nota (1973), was used to determine substratum type at each sampling station (Appendix 3). It clearly identifies the dominant depositional process such as relict pelite and residual sand. The original sediment classification was kept, with 46 substratum codes identified by textual analysis. As an example, pelite, sandy-pelite and gravel-shell were three of the principal substratum composition found in the St. Lawrence (Appendix 3). Maximal bottom current was also included as an abiotic factor. This variable was provided by the circulation model simulation implied rivers, atmospheric and oceanographic forcing (Saucier *et al.*, 2003). At each sampling station, the bottom current value was obtained daily for 31 days in August and the maximal value at each station was included to the subsequent analysis.

1.2.4 Statistical analyses

Data were analysed by multivariate approach using the V5 PRIMER Analytical Package (Clarke and Warwick, 1994). The multivariate procedure on species assemblages was based on the Bray-Curtis dissimilarity on square-root ($\sqrt{}$) data transformed and presence/absence (P/A) community data. This intermediate transformation was chosen in order to provide the best balance between a "narrow view" of community structure based on abundance of few dominant taxa and a "wide view" based on all species, giving too much weight on rarest taxa (Clarke and Warwick, 1994). Prior to analyses, taxa which appeared once or were associated with only one station

were excluded from the dissimilarity matrix, as suggested by Clarke and Warwick (1994). Differences in the structure of epibenthic macrofaunal assemblages along the Estuary and the Gulf of St. Lawrence were examined using non-metric multidimensional scaling (nMDS) ordination technique. Ordinations were based on the Bray-Curtis dissimilarity measure (Bray and Curtis, 1957). The SIMPER routine (similarity percentage analysis) was used to determine which species were predominantly responsible for the dissimilarity within groups, and to characterize each assemblage (Clarke, 1993).

Multivariate ordination techniques were also applied to analyse the spatial variation in the species abundance data sets, using CANOCO 4.5 program (ter Braak and Smilaeur, 2002). Canonical correspondence analyses (CCA) were calculated on: 1) biomass database, 2) abundance database and on 3) a database included both biomass and abundance data, to explore the relationship between the observed macrofauna assemblages and their environment (CANOCO, ter Braak and Smilaeur, 2002). A preliminary detrented correspondence analysis (DCA with detrending by segments) was applied to estimate the gradient length in standard deviation (SD) units. Gradient values exceeding 3 SD were obtained in each case, and then subsequent numerical analyses involved techniques were based on underlying unimodal species-response model (Jongman *et al.*, 1995; Leps and Smilauer, 2003). Statistical associations between species macrofaunal assemblage patterns and environmental parameters were further quantified by canonical correspondence analysis (CCA), a non-linear eigenvector ordination technique related to CA, but where the axes corresponding to the directions of the

greatest data set variability can be explained by the environmental variables (ter Braak, 1986). A table of explanatory variables was obtained to examine the amount of variation explained in the species data that was associated with the environment. CCA was then carried out followed by a Monte-Carlo permutation test, using 999 permutations with forward selection (ter Braak, 1989). This procedure was used to rank the environmental factors by importance and to selected, one at a time, significant factors which were maximally correlated with species distribution. Matrices with inter-set correlation values between environmental variables and axes where obtained, which one determines principal environmental gradients in the ordination plan. Statistical significant values of environmental parameters were also obtained, with the conditional effect ($P < 0.01$). Plots results were made using drawing program CanoDraw 4.12.

1.2.5 Geostatistics and GIS mapping

The raster map of spatial distribution of environmental parameters and community patterns was produced using the kriging method. Model fit and kriging were carried out using GENSTAT 7th edition software (GENSTAT committee, 2003) (Appendix 4). Kriged estimate resulted as fine regular grid of points, was then imported in Arcmap 9.1 (ESRI) software. Raster continuous maps with a resolution of 0.008 decimal degrees, displaying the spatial pattern of each variable (environmental) were created, using the spatial analyst extension (Appendix 5).

1.2.6 Predictive ecological model of community habitat

As preliminary step of modelling, a combination of both data sets was made (abundance and biomass) and the abundance data were fourth root ($\sqrt{\sqrt{}}$) transformed prior to analysis, to reduce the effect of abundant species (Clarke and Green, 1988). Axes samples scores of canonical analyses and the significant variables found in the CCA as explanatory variables were used in the Gaussian (transformed data) GLM model. As suggested by McCullagh and Nedler (1989), a generalized linear model (GLM) was the approach chosen to model the community structure as a response of the environment. This kind of model may be applied to data that are not necessarily normally distributed. The modelling procedure was performed in R software. The stepwise selection of significant predictors was based on the Akaike's Information Criterion (AIC) (Akaike, 1974). Equations obtained inform the model then used in the Raster calculator option in ArcMap, to produce a predictive model of benthic organisms (Appendix 6).

1.3 Results

1.3.1 Epibenthic macrofauna

Over 160 epibenthic taxa (124 for the abundance database and 60 for the biomass database) in 97 families, 50 orders, 21 classes and 10 phyla were recorded during the survey. A high proportion of species were associated with phyla of polychaetes,

echinoderms, cnidarians, molluscs and arthropods. Members of sipunculids, nematods, brachiopods and ectoprocts were also found.

The total number of epibenthic species was higher in the Strait of Belle Isle and the northern part of Esquiman channel, with a maximum of 32 species per trawl tow (Fig. 2). Particular diversity spots are found at many sampling stations localised on the north shore of the Gulf, near Mingan Island and Natashquan region (Quebec North Shore). The trawl stations of these two areas were in water of less than 100 m deep. The collected mean number of species (15 ± 2 per trawl tow) is also important off the southwest coast of the Newfoundland (Fig.2). Conversely, the main part of the Esquiman channel exhibited low species richness, with a mean number between two and six species per trawl tow. A great part of Laurentian channel was also characterized by a small number of species, excluding the region at the head, near the Saguenay fjord, where species richness was higher.

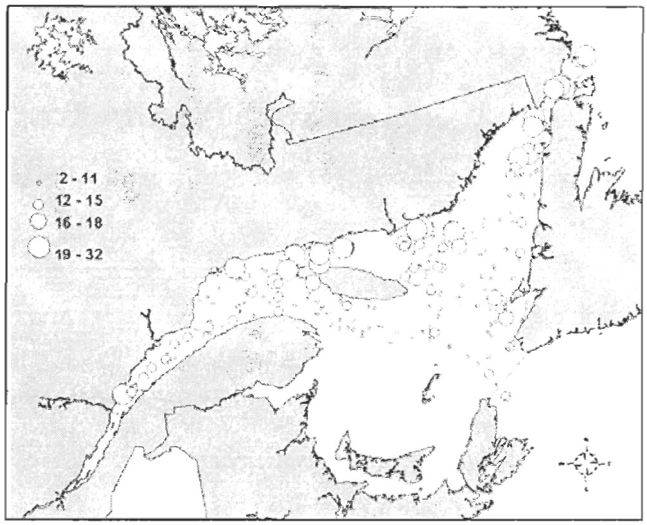

Figure 2. Total number of macrofauna species caught with the Campelen bottom trawl, in the Estuary and the northern Gulf of St. Lawrence during the annual summer survey in August 2006.

1.3.2. Macrobenthic community structure

Cluster analysis, based on square root transformed data, divided the biomass fauna database (kg/km^2) into seven distinct communities. Most stations were grouped (five groups) at 70% of dissimilarity and two others at 55%. Multivariate macroinvertebrate assemblages showed two main distinct groups with a particular species distribution. A distinct community (group V:□) was spatially located with majority of stations in the Estuary. Group IV (▲) also showed a distinct wide spectrum of assemblage scattered over the Laurentian and Esquiman channels. Community of Groups I, II, III, VI and VII, smaller than Groups V and IV, were punctually distributed and closer spatially, over the study area (Fig. 3). Group I (○) indicated a specific distribution divided in two main spots, in the Strait of Belle Isle and near Mingan Island. The greatest dissimilarity

between groups (SIMPER analysis) was observed with Group V relative to all other groups, and was characterized by the high contribution of Actiniaria, *Ctenodiscus crispatus* and *Brisaster fragilis*. Scyphozoa and *Illex* sp. were the macrofauna taxa characterizing group IV (▲) (Table 1).

Cluster analysis based on the abundance database (ind/km^2), suggested the first five groups at 95% of dissimilarity with another two groups (II: ■ and III: ▼) distinct at 90%. Groups I (○) and II (■) were the smallest, based on two stations. Group I was located on the southwestern part of the Newfoundland whereas Group II was found at the head of the Laurentian channel. Group V (□) was distributed from the Estuary through the Cabot Strait (Fig. 4). SIMPER analysis revealed that a high contribution of similarity from a particular species was found in each group. For example, *Hippasteria phrygianna* contributed 63,06% in Group IV, while *Syscenus infelix* was 73,77% in Group V (Table 2).

With regards to the occurrence database (P/A), the five groups were well-dispersed over the study area (Fig. 5). We also observed the same community composition (Group IV: ▲), using the observed abundance database, ranging from the Laurentian Channel out to the Atlantic Ocean beginning at Cabot Strait (Fig. 5). The same aggregated group near the Strait of Belle Isle and the Mingan Islands was also founded (Group I: ○), but stations of western part of Newfoundland were also included in this group. The results of

SIMPER analysis showed a similar average for the five clusters, with a similar contribution among the species (Table 3).

Futhermore, the three nMDS plots (occurence, biomass and density) showed similar community distribution over the study area. These are: (1) the same aggregated group was found near Mingan Island and Strait of Belle-Isle; (2) the same community composition ranging from the Laurentian Channel out to the Atlantic Ocean beginning at Cabot Strait, and finally; (3) a mix of community assemblages was found at two specific locations at the northeastern and the northwestern end of Anticosti Island.

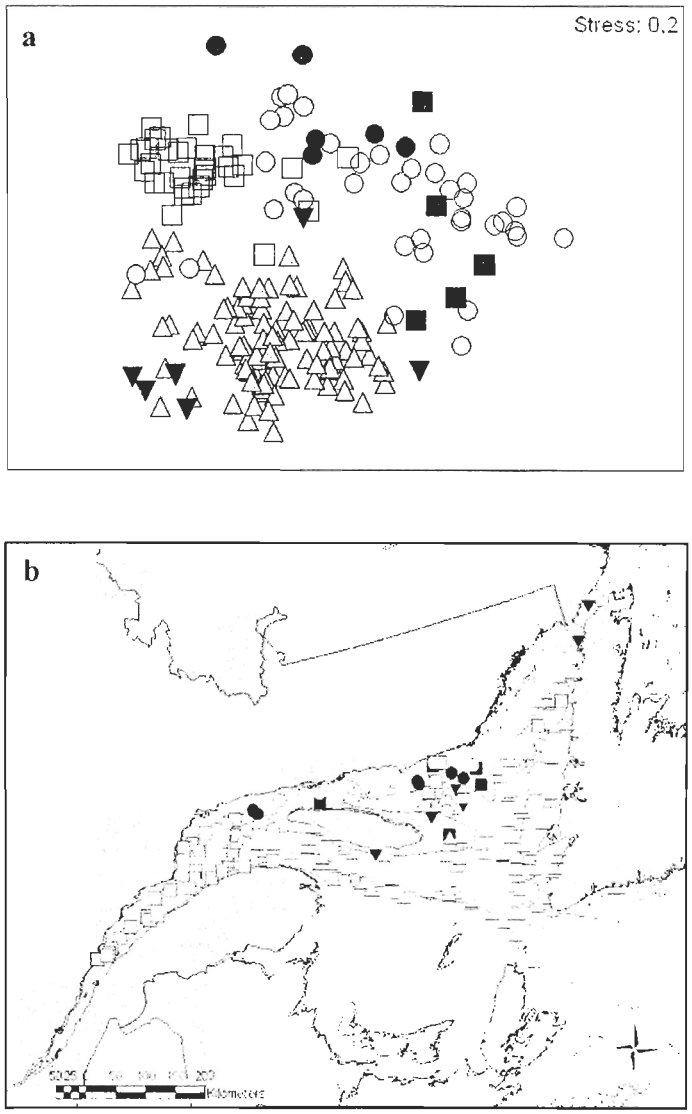

Figure 3. Epibenthic macrofauna community (biomass database) in the St. Lawrence in August 2006. a) Non-metric multidimensional scaling (nMDS) ordination based on the Bray Curtis dissimilarity, square-root transformed data ($\sqrt{x}$). b) Location of clusters in the study area (empty circle = group I, black square = group II, black down triangle = group III, grey triangle = group IV, empty square = group V, grey circle = group VI and black circle = group VII).

Table 1. Result of SIMPER analyses showing the macrofauna taxa which contributed the most to the average Bray-Curtis similarity within the clusters of biomass database (all trawling stations), based on square root transformed density.

Species	Contr. (%)	Species	Contr. (%)
Group I (Avg. similarity = 36.19)		**Group II** (Avg. similarity = 35.22)	
Gorgonocephalus arcticus	46.43	*Ophiopholis aculeata*	57.40
Boltenia ovifera	36.18	*Gorgonocephalus arcticus*	12.80
Ophiopholis aculeata	4.86	*Gersemia* sp.	11.74
Gersemia sp.	4.09	*Ophiacantha bidentata*	11.04
Group III (Avg. similarity = 50.81)		**Group IV** (Avg. similarity = 41.99)	
Illex sp.	91.15	Scyphozoa	58.86
		Illex sp.	26.69
		Actiniaria	4.62
Group V (Avg. similarity = 45.32)		**Group VI** (Avg. similarity = 49.89)	
Actiniaria	58.34	*Bolocera* sp.	84.88
Ctenodiscus crispatus	15.44	*Hormathia nodosa*	4.39
Brisaster fragilis	13.26	*Ctenodiscus crispatus*	2.51
Bolocera sp.	5.86		
Group VII (Avg. similarity = 33.73)			
Ctenodiscus crispatus	67.67		
Hormathia nodosa	18.99		
Gersemia sp.	3.84		

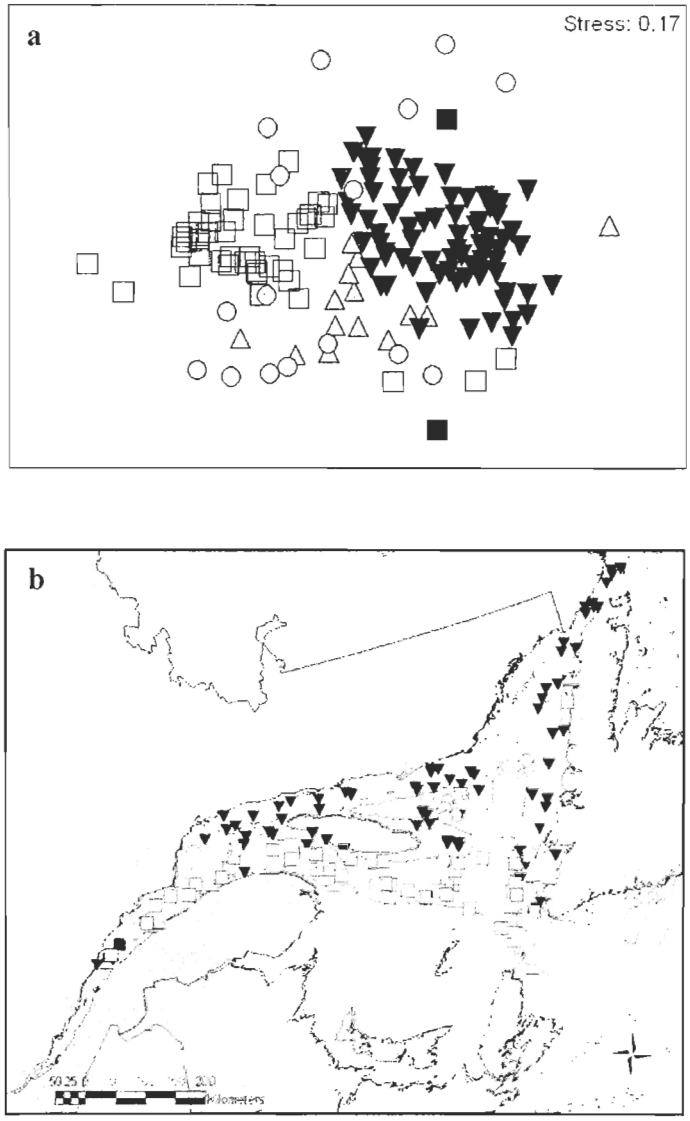

Figure 4. Epibenthic macrofauna community (abundance database) in the St. Lawrence in August 2006. a) Non-metric multidimensional scaling (nMDS) ordination based on the Bray Curtis dissimilarity, square-root transformed data (√x). b) Location of clusters in the study area (empty circle = group I, black square = group II, black down triangle = group III, grey triangle = group IV, empty square = group V and grey circle = group VI)

Table 2. Result of SIMPER analyses showing the macrofauna species which contributed the most to the average of Bray-Curtis similarity within the clusters of abundance database (all trawling stations), based on square root transformed density.

Species	Contr. (%)	Species	Contr. (%)
Group I (Avg. similarity = 33.00)		**Group II** (Avg. similarity = 35.81)	
Aporrhais occidentalis	100	*Buccinum totenie*	57.87
		Mytilus edulis	24.68
		Megayoldia thracieformis	17.45
Group III (Avg. similarity = 21.98)		**Group IV** (Avg. similarity = 21.23)	
Henricia sp.	38.22	*Hippasteria phrygianna*	63.06
Strongylocentrotus sp.	28.23	*Buccinum undatum*	7.44
Crossaster papposus	6.12	*Henricia* sp.	6.56
Rhachotropis aculaeta	5.38	*Strongylocentrotus* sp.	5.25
Pteraster pulvillus	5.21	*Nymphon macrum*	4.67
Buccinum undatum	2.82	*Megayoldia thracieformis*	3.63
Group V (Avg. similarity = 30.96)		**Group VI** (Avg. similarity = 18.40)	
Syscenus infelix	73.77	*Cuspidaria glacialis*	71.13
Munidopsis curvirostra	18.71	*Molgula* sp.	10.34
		Ciona intestinalis	4.65
		Aporrhais occidentalis	2.84
		Hippasteria phrygianna	2.67

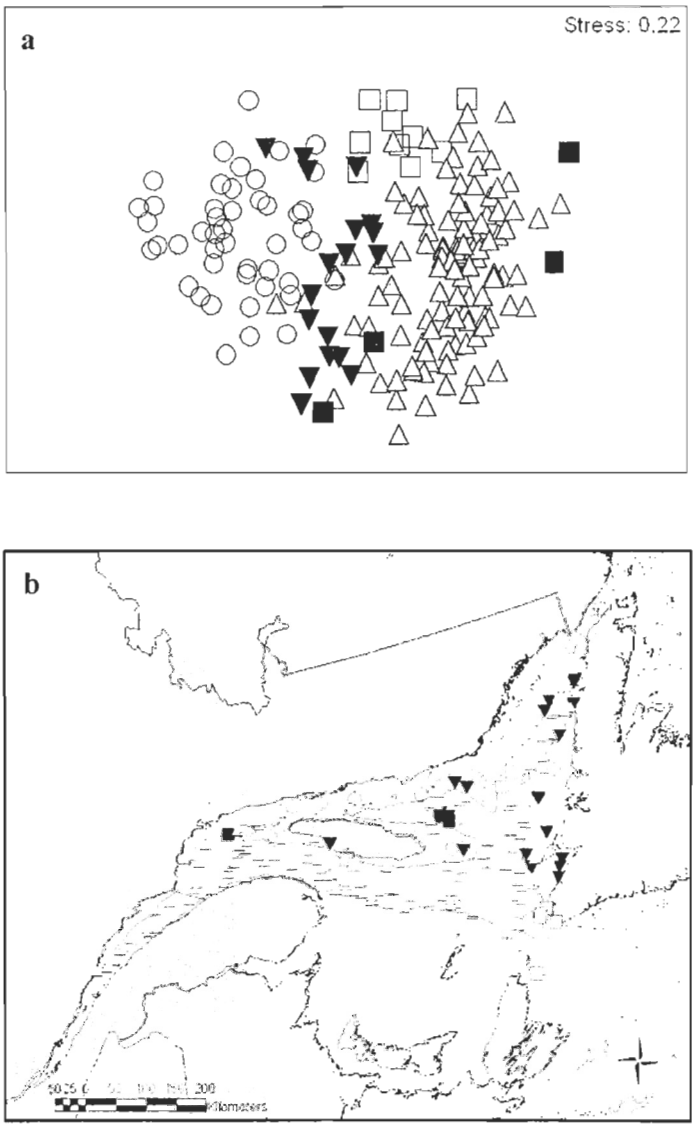

Figure 5. Epibenthic macrofauna community in the St. Lawrence in August 2006 a) Non-metric multidimensional scaling (nMDS) ordination based on the Bray Curtis dissimilarity, Presence/Absence (P/A) transformed data. b) Location of cluster in the study area (empty circle = group I, black square = group II, black down triangle = group III, grey triangle = group IV, empty square = group V)

Table 3. Result of SIMPER analyses showing the macrofauna species which contribued the most to the average of Bray-Curtis similarity within the clusters (all trawling stations), based on presence/absence transformed density.

Species	Contr. (%)	Species	Contr. (%)
Group I (Avg. similarity = 35.81)		**Group II** (Avg. similarity = 35.93)	
Strongylocentrotus sp.	12.74	*Bolocera* sp.	29.55
Ophiopholis aculeata	11.73	Sepiolidae	15.57
Henricia sp.	10.04	*Hormathia nodosa*	15.57
Crossaster papposus	7.91	*Ciona intestinalis*	15.57
Rhachotropis aculaeta	7.19	Scyphozoa	4.88
Scyphozoa	6.90	*Cuspidaria glacialis*	4.88
Group III (Avg. similarity = 36.66)		**Group IV** (Avg. similarity = 39.01)	
Scyphozoa	28.45	Scyphozoa	14.64
Ctenodiscus crispatus	16.25	Actiniaria	13.91
Henricia sp.	11.01	*Brisaster fragilis*	13.55
Strongylocentrotus sp.	9.51	*Ctenodiscus crispatus*	12.98
Ophiopholis sarsi	4.88	*Illex* sp.	11.30
Hippasteria phrygianna	4.45	*Pennatula* sp.	11.02
Group V (Avg. similarity = 39.72)			
Illex sp.	29.78		
Scyphozoa	22.01		
Gersemia sp.	20.03		
Pennatula sp.	7.63		
Bathypolypus sp.	5.75		
Antedon bifida	2.92		

1.3.3 Pattern analysis

To identify environmental parameters responsible for macrobenthic community distribution from set of ecological data, the first step was to identify patterns of the species abundance. As preliminary steps, gradients lengths were explored at constrained canonical analysis to estimate the standard deviation. Detrended correspondence analysis (DCA), detrending by segments, gives values between 3.28 to 7.24 SD, and therefore unimodal methods of ordination were used for subsequent analyses. DCA was applied to macrobenthic databases (abundance, biomass and occurence) and also to SIMPER species abundance database which are taxa that account for 15% and more to the similarity within the groups. Incidentally, canonical correlation (CCA), combined with numerical analysis, can reveal the ecological preference of species colonizing the study habitat.

Canonical correspondence analyses (CCA) with Monte Carlo permutation and the forward selection option were performed to test the significance of the relationships of the samples and species to the available environmental parameters. The inter-sample and Hill's scaling were choosen for the CCA on the abundance data sets. Hill's scaling is more appropriated to a strong unimodal response for long gradient. In summary, species which occurred at the station lie around the sample's point in the plot (Leps and Smilauer, 2003).

When examining the assemblages of the biomass abundance database, a CCA showed significant relationship ($p < 0.01$) with eight environmental parameters. These are: oxygen saturation, depth, maximal bottom current, and five sediment types (pelite, very sandy-pelite, gravel-shell, gravelly-pelite-sand and gravelly-sandy-pelite). First principal CCA axis accounted for 39.60% and 28.30% for the second axis, these together accounted for 67.90% of the relationship between species and environmental parameters (Table 4a). The presence of gravel and pelite appeared an important factor on the first axis, with high correlation values (0.42) with gravelly-pelite-sand and gravel-shell. On the second axis, very sandy pelite substratum was the highest positively correlated factor (0.36), whereas five of eight environmental variables were negatively correlated. The group V (□) was primarily influenced by three factors: depth, presence of pelite (P), and very sandy pelite (VSP) sediment (Fig.6). Group I (○), distributed on the upper right corner of the CCA graph, appeared to be impacted by high oxygen saturation and presence of gravel (gravel-shell (GSh) and gravelly-pelite-sand (GPS)). Group IV (▲), with the greatest number of stations, was influenced principally by medium to high oxygen saturation value. This group was also impacted by bottom current (Fig. 6). Groups I (○) and IV (▲), found on the right side of the ordination, indicated distinctive macrobenthos composition in comparison with Group V (□) principally located on the left side.

Each variable was tested in turns and bottom maximal current, depth and five sediment types (pelite (P), sandy-pelite (SP), very-sandy-pelite (VSP), calcareous-pelite (CP) and gravel-shell (G-Sh)) were found significantly related to the assemblage structure of abundance database. The first and second axes account together for 41.6% (first axis: 24%, second axis: 17.6%) of the relation between species and environmental conditions (Table 4b). The calcareous-pelite sediment showed the highest positive correlation along the first axis with a value of 0.58, followed by depth with 0.46, whereas the gravel-shell sediment factor correlation was highly negative (-0.32). With the second CCA axis, the maximum absolute correlation was recorded with very-sandy-pelite substratum factor, followed by pelite and sandy-pelite, 0.70, 0.12 and 0.02 respectively. In contrast, all other factors were negatively correlated (Table 4b). In this setting, the largest Group III (▼) had an important number of stations influenced by low to intermediate bottom current and depth value, but the total distribution was scattered among the seven environmental parameters (Fig. 7). Groups IV (▲) and VI (●) were represented largely by the same ecological niche, with a direct influence on species by the abiotic factors found at the right side of the CCA graph (pelite sediment, depth and bottom current). Indeed, in the perpendicular direction, stations of these two groups cut the depth and current arrows at the same intermediate to high values. A number of stations owned to Group V (□) were locally isolated to the bottom right of the ordination, near the calcareous-pelite (CP) environmental factor, with high depth values. This distribution pattern indicated a distinctive macrofaunal composition in comparison with the others groups as reported in table 2.

CCA was also calculated on $\sqrt{\sqrt{}}$ transformed data (abundance and biomass) (Table 4c). First and second principal CCA axes accounted for 39.1% of the relationship between species and environmental parameters, and the first one showed the highest correlation with 22.3%. Substratum composition of gravel-shell was strongly related with the first CCA axis (0.50), whereas temperature, oxygen saturation and depth were strongly negatively correlated, with -0.46, -0.44 and -0.42 respectively. As indicated on the ordination plan, the direction and the magnitude of temperature and depth were very similar whereas oxygen saturation was inversely correlated, with low oxygen value when depth and temperature were high. Besides, very-sandy-pelite substratum was strongly associated with the second CCA axis (0.78), while eight abiotic factors were negatively correlated. The arrangement of samples in relation to the ten environmental parameters illustrated two distinct spatial plans (Fig.8). Samples to the right of the ordination were strongly correlated to oxygen and substratum composition of gravel (gravel-shell (GSh) and gravelly-pelite-sand (GPS)). Conversely, samples to the left were more associated with depth, temperature, current and substratum composition of pelite (VSP, P, SP, CP) (Fig. 8). The largest group, IV (▲), found on the left side of the ordination plan, indicated a large variety of ecological niche. Stations of this group were found at different values of depth, temperature and bottom current. Group III (▼) and group I (○) were principally found on the right side or the ordination plan.

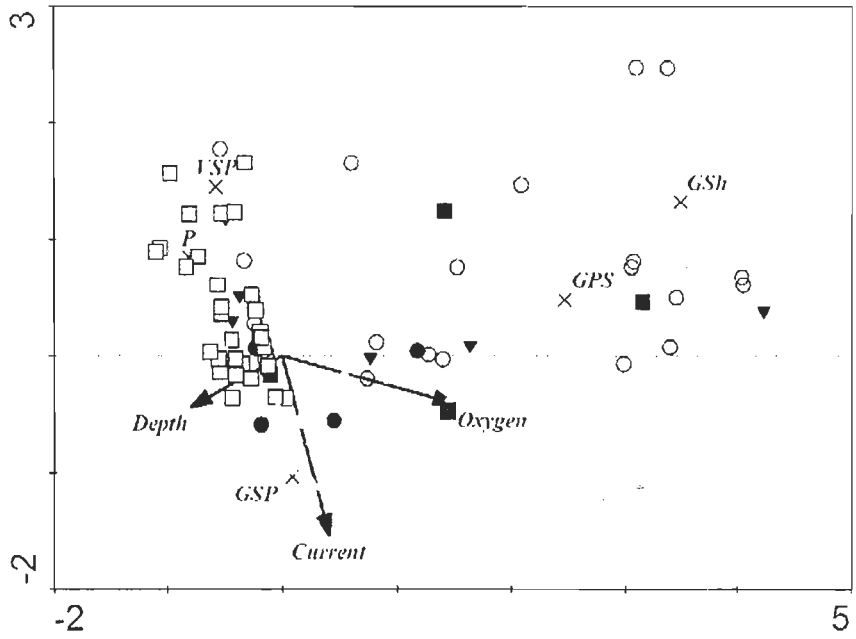

Figure 6. Results for calculated canonical correspondence analyses (CCA) of epibenthic macrofauna sampling stations and corresponding environmental factors. CCA was calculated for √-transformed biomass data (kg/km2 database) and matrix of eight significant environmental variables tested. The arrows and X mark indicate significant explanatory variables, with the arrowheads indicating the increase in gradient. Groups legend: empty circle = group I, black square = group II, black down triangle = group III, grey triangle = group IV, empty square = group V, grey circle = group VI and black circle = group VII. Substrata legend: P = pelite, VSP = very-sandy-pelite, GSh = gravel-shell, GPS = gravel-pelite-sand, GSP = gravel-sandy-pelite

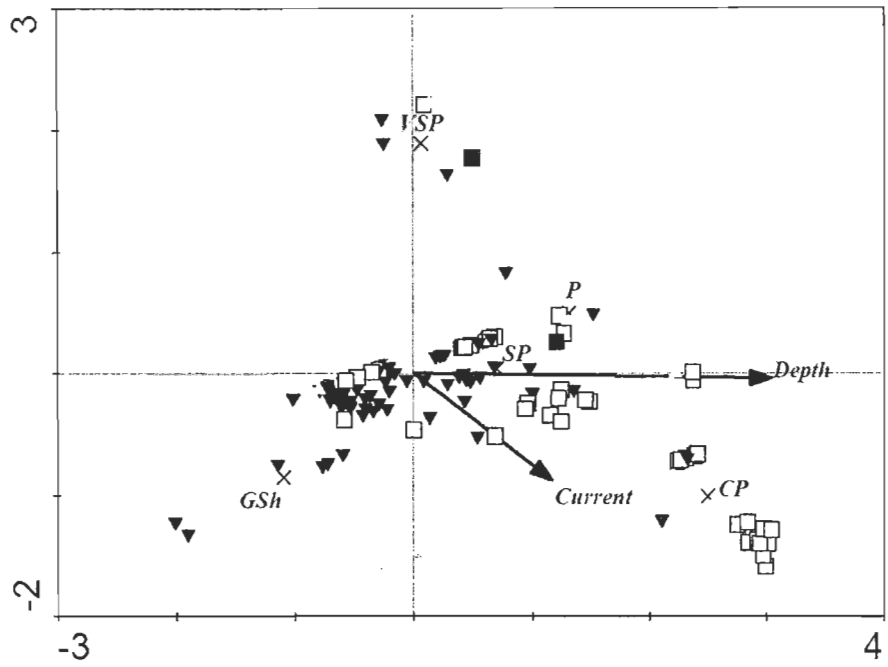

Figure 7. Results for calculated canonical correspondence analyses (CCA) of epibenthic macrofauna sampling stations and corresponding environmental factors. CCA was calculated for √-transformed abundance data (ind/km2 database) and matrix of seven significant environmental variables tested. The arrows and X marks indicate significant explanatory variables, with the arrowheads indicating the increase in gradient. Groups legend: empty circle = group I (hide), black square = group II, black down triangle = group III, grey triangle = group IV, empty square = group V and grey circle = group VI. Substrata legend: GSh = gravel-shell, VSP = very-sandy-pelite, P = pelite, SP = sandy-pelite, CP = calacareous-pelite.

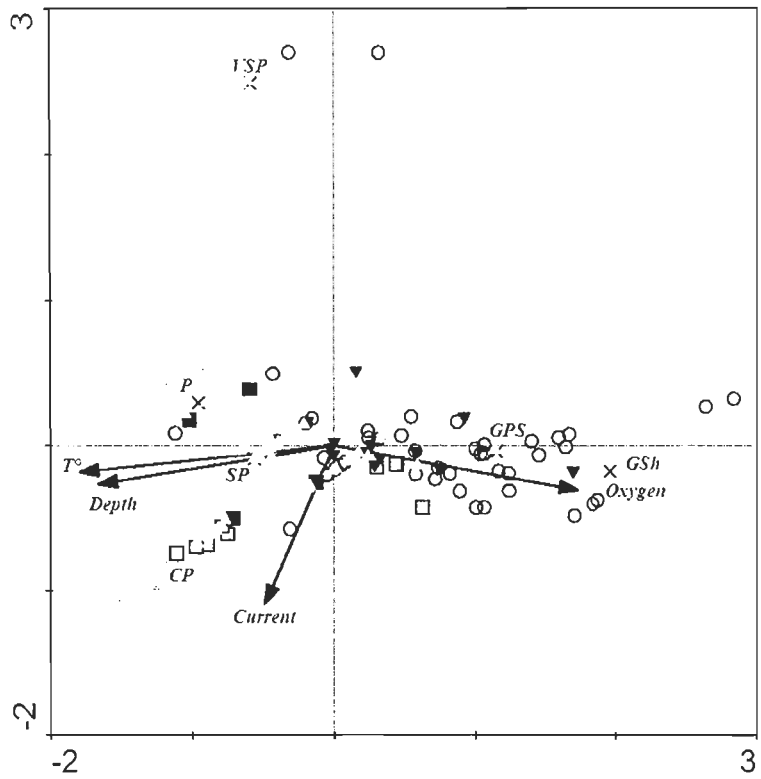

Figure 8. Results for calculated canonical correspondence analyses (CCA) of epibenthic macrofauna sampling stations and corresponding environmental factors. CCA was calculated for √√ transformed data (abundance and biomass) and matrix of ten significant environmental variables tested. The arrows and X mark indicate significant explanatory variables, with the arrowheads indicating the increase in gradient. Groups legend: empty circle = group I, black square = group II, black down triangle = group III, grey triangle = group IV, empty square = group V. Substrata legend: CP = calcareous-pelite, SP = sandy-pelite, P = pelite, VSP = very-sandy-pelite, GPS = gravel-pelite-sand, GSh: gravel-shell.

Table 4. Results for two calculated canonical correspondence analyses (CCA) on: a) biomass database: b) abundance database: c) occurence database, including the Monte Carlo permutation tests of macrofauna species abundance and corresponding environmental factor, with the conditional effect summary, are also included.

a) Axes	Axis 1	Axis 2
Eigenvalues	0.41	0.29
Species-environment correlations	0.74	0.72
Cumulative percentage variance		
of species data	8.60	14.70
of species-environment relation	39.6	67.9

Environmental variables	Inter-set correlations		Conditional effects	
	Axis 1	Axis 2	P	F
Current	0.11	-0.42	0.002	7.24
Oxygen	0.39	-0.12	0.002	2.61
Depth	-0.21	-0.12	0.002	4.52
Pelite	0.39	-0.11	0.004	4.42
Gravelly-sandy pelite	0.02	-0.30	0.002	5.81
Gravelly-pelite-sand	0.42	0.10	0.002	7.14
Very sandy pelite	-0.11	0.36	0.002	6.69
Gravel-shell	0.42	0.20	0.002	4.18

b)Axes	Axis 1	Axis 2
Eigenvalues	0.49	0.36
Species-environment correlations	0.83	0.82
Cumulative percentage variance		
of species data	3.00	5.30
of species-environment relation	24.0	41.6

Environmental variables	Inter-set correlations		Conditional effects	
	Axis 1	Axis 2	P	F
Current	0.17	-0.14	0.002	2.13
Depth	0.46	-0.01	0.002	1.70
Pelite	0.25	0.12	0.002	3.16
Calcareous pelite	0.58	-0.30	0.002	3.51
Sandy pelite	0.23	0.02	0.002	2.16
Very sandy pelite	0.02	0.70	0.002	3.22
Gravel-shell	-0.32	-0.33	0.004	2.56

c) Axes	Axis 1	Axis 2
Eigenvalues	0.49	0.37
Species-environment correlations	0.85	0.86
Cumulative percentage variance		
of species data	3.00	5.30
of species-environment relation	22.3	39.1

Environmental variables	Inter-set correlations		Conditional effects	
	Axis 1	Axis 2	P	F
Current	-0.12	-0.29	0.002	2.97
Depth	-0.42	-0.07	0.002	2.06
Temperature	-0.46	-0.05	0.002	1.90
Oxygen	-0.44	-0.08	0.002	2.28
Pelite	-0.23	0.09	0.002	2.63
Calcareous-pelite	-0.38	-0.33	0.002	1.64
Sandy-Pelit	-0.24	-0.05	0.004	1.53
Very-sandy-pelite	-0.14	0.78	0.002	4.22
Gravelly-pelite-sand	0.30	-0.01	0.002	2.37
Gravel-Shell	0.50	-0.06	0.002	3.75

1.3.4 Influence of oxygen on macrobenthic community structure

The total density of three specific taxa (crustaceans, molluscs and cnidarians) collected at the different sampling stations of the study area was illustrated with the spatial pattern of oxygen saturation (Fig. 9). Thus, the density values of these three taxa were different at the Lower St. Lawrence Estuary (LSLE) stations where hypoxia was observed (oxygen saturation value near 20%). Indeed, the proportions of molluscs and cnidarians were most important in the LSLE, comparatively to the crustaceans.

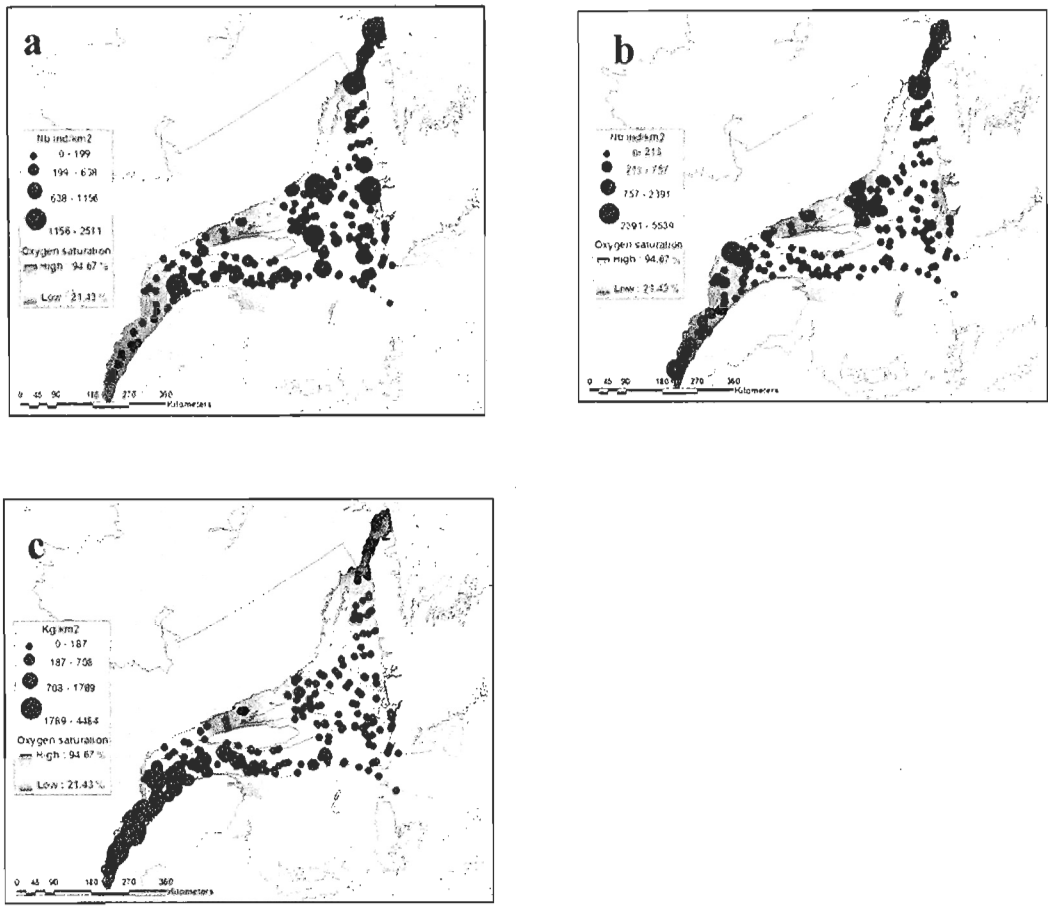

Figure 9. Distribution of macrobenthic taxa of: a) crustaceans; b) mollusks; c) biomass of cnidarians, in the study area. Background colors showed the spatial distribution of oxygen saturation. Circle diameter indicates the scale of the abundance

1.3.5 Generalized linear model

The relationship between the community structure and environmental parameters recorded at each trawling station was modelled using a Generalized Linear Model (GLM). By this technique, we tried to predict community composition from environment parameters, resulting in a potential map of macrobenthic habitat type. Preliminary canonical analysis (CA) and CCA were executed using the combined fourth-root transformed abundance and biomass data (Legendre and Legendre, 1998). The species-environment relationship was higher with the fourth-root transformation and was then kept to produce the model. The first two axis sample scores of the CA of the abundance stations in the study area and the significant environmental variables found in CCA were used in this GLM model. Second order polynomials were introduced to the model in order to best illustrate the relationship with environmental parameters. The final model was based on stepwise selection of significant variables using the Akaike Information Criterion (AIC) (Vaz *et al.*, 2005).

The final ecological model of axis 1 sample score retained four environmental variables as significant. According to AIC, depth, bottom current, mean temperature and oxygen saturation were introduced in the model. The second order was used for depth, temperature, bottom current and oxygen to improve the model. The regression coefficients of the model indicated that all parameters were significantly correlated (Spearman correlation; $p < 0.05$) (Appendix 6). The strongest correlation values were obtained with temperature and depth parameters.

Axis 1 ~ oxygensaturation^2 + depth + depth^2 + temperature + temperature^2 + bottomcurrent^2

Axis 2 ~ chlorophyll + chlorophyll^2 + oxygensaturation + oxygensaturation^2 + depth + depth^2 + temperature + temperature^2 + bottomcurrent + bottomcurrent^2 + substrata

The final ecological model for axis 2 sample score included all the environmental variables studied in the project, but most of them were non significant ($p > 0.05$) (Appendix 6). The final model of axis 2 was thus rejected to illustrate the community species/environment relationship. Only the model predicted by CCA axis 1 was retained for further analysis.

The resulting benthic habitat suitability map is illustrated in figure 10. Areas of high suitability values were predicted in: (1) Mingan Island and northwestern end of Anticosti Island; (2) on the Quebec Lower North Shore near Beaugé Bank; (3) at the head of the Esquiman channel to Belle Isle: and finally (4) at two locations on the southwestern coast of Newfoundland. Conversely, the Laurentian and Esquiman channels had lower values. Finally, the Atlantic Ocean entry at Cabot Strait recorded the lowest data. This habitat suitability map shows good agreement with the map of species richness (Fig. 2). A difference between values measured on CA axis with macrofauna sampling during the survey and values estimated by the model at the same station was calculated. The difference was then divided by the highest value found with the data survey. An estimation error map was produced to illustrate the measure of the model fit over the

study area (Fig. 11). The continuous map resulting from the kriging interpolation showed a high predicted error value in the Cabot Strait near the mouth of the Laurentien channel and near the north Shore of Anticosti Island. These values can be explained by the small number of fishing stations and also by the presence of hard trawlable bottom. Area with a too small number of sampling stations cannot give a good interpolation of the reality.

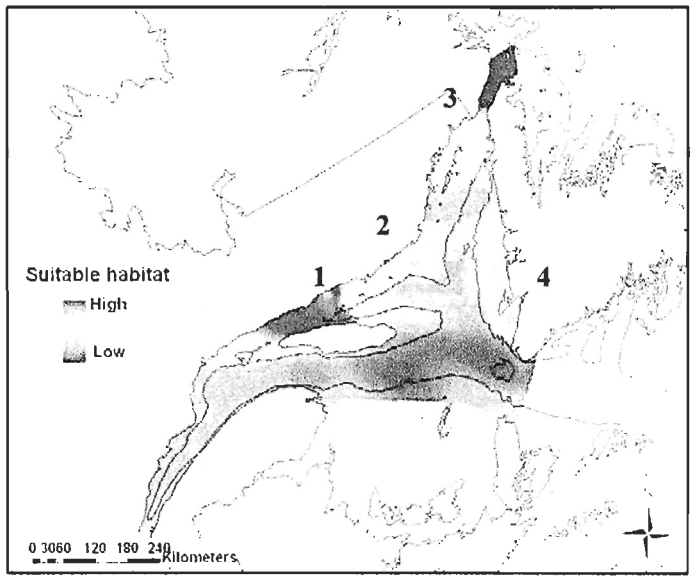

Figure 10. Predicted preferential habitat model (GLM) of epibenthic macrofauna community of the Estuary and the northern Gulf of St. Lawrence, resulted from the first CA axis.

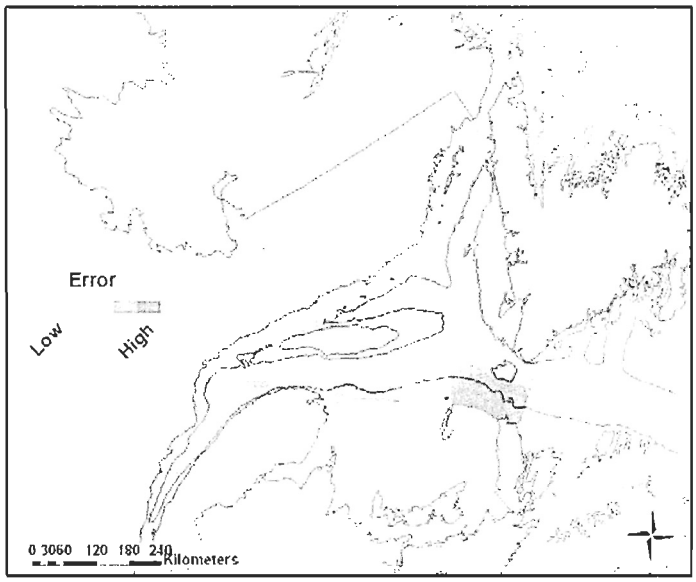

Figure 11. Predicted error map of the preferential habitat model of epibenthic macrofauna of the Estuary and the northern Gulf of St. Lawrence.

1.4 Discussion

This study improved our knowledge about the benthic macrofaunal ecosystem by using a combined multivariate and geostatistical approach. Globally, the results can be summarized in three main points: (1) the distribution of the macrofauna community structure is spatially variable over the St. Lawrence Gulf and Estuary, and the multivariate analysis revealed eight different assemblages; (2) according to canonical analysis, these patterns are related to prevailing environmental variables (depth, temperature, oxygen, bottom current and sediment type); (3) hypoxic condition affects differently benthic organisms community structure and; (4) habitat suitability model is used to relate communities structure to the significant environmental parameters found by GLM (depth, temperature, oxygen and bottom current). These results represent an important baseline for the future marine conservation management activities for the Gulf and St. Lawrence Estuary.

1.4.1 Macrobenthic community structure

An important boundary between the different assemblages in the Estuary and the northern Gulf of St. Lawrence was observed. The multivariate analysis differentiated eight biogeographic zones over the study area. This division was based on the species richness and spatial distribution maps of the different benthic organisms.

The cluster analysis allowed a division of the Estuary and the northern Gulf of St. Lawrence similarly to previous biogeographic regions decribed by Brunel *et al.* (1998). However, according to the results of the current study, the Middle North Shore (MCN) described by Brunel *et al.* (1998), should be divided in two specific biogeographic zones. This is in agreement with the production units of snow crab (Fig. 5, in Sainte-Marie *et al.*, 2005). This characterization was based on the natural boundaries of the seabed topography of the St. Lawrence ecosystem. As noted in few studies, the St. Lawrence ecosystem should not be viewed as a homogeneous system, and previous authors also divided this ecosystem into sections based on hydrodynamic, physical and biogeographic conditions (Koutistonsky and Bugden, 1991; Brunel *et al.*, 1998; Bourget *et al.*, 2003). Moreover, Bourget *et al.* (2003) mentioned that the community structure is spatially patterned and the cause of this patchiness could differ from zone to zone in the Estuary and the northern Gulf of St. Lawrence.

The grouping method revealed distinctive differences between deep channel macrofauna assemblages and the shallower areas, whereas sub-communities where defined in regions where specific hydrodynamic and environmental conditions such as upwelling, and tidal-mixing, were found. The Northwest Gulf community defined by Sainte-Marie *et al.*, (2005), located near the Mingan Island and the Strait of Belle-Isle community, was located in specific area with major structures in the circulation patterns of the St. Lawrence, which can have an important influence on the benthic community distribution. Mingan Island area is characterized by a strong tidal-mixing and wind-induced coastal upwellings and eddies (Le Fouest, 2005), while topography and wind

interaction in the southern Strait of Belle-Isle create a productive upwelling zone (Rose and Legett, 1988). Moreover, the mixing of the St. Lawrence water with the Labrador Shelf Water, which enters via the Strait of Belle-Isle (Houghton and Fairbanks, 2001), could also be favourable to benthic organisms mixing of those two water types. The presence of these dynamic conditions in these two areas could partly explain why similar species composition was observed. Besides, this assemblage was also found on the west coast of Newfoundland (TNO division of Brunel *et al.,* 1998) in the occurence and abundance databases. These groups were located between depth contours < 200 m. This assemblage was characterized by the presence of many free-living species (*Strongylocentrotus* sp., *Henricia* sp., *Crossaster papposus, Gorgonocephalus* sp., and *Rhachotropis aculeate*) and sessile species (*Boltenia ovifera* and *Gersemia rubiformis*). It is not surprising to find the predator *C. papposus* in the same area than *Strongylocentrotus* sp. as this echinoderm has often been observed feeding on urchins (Coleman, 1991).

Thouzeau *et al.* (1991) concluded that significant differences observed in the benthic composition of the Eastern Georges Bank follow smaller variation in sediment type, and suggested that sediment type could be the key factor explaining the benthic distribution. Thus, the presence of gravel in the substrata of many stations near Mingan Island and in the Strait of Belle-Isle community may explain the occurrence of sessile organisms anchored to the seabed sediment (Appendix 3). The zonation of this particular macrofauna assemblage is in accord with differences in the general nature of the sediment, as classified by Loring and Nota (1973) for the study area. Indeed, CCA

revealed that the specific assemblage of Group 1 (biomass database), with presence of *B. ovifera* and *Gersemia* sp., was structured according to sand and gravel. Stations of the study area are predominantly composed of fine-grain sediment, and this presence of coarser substrata at these specific seabed zones can have an effect on the macrofauna composition.

A distinct macrobenthic community was distributed along the Lower St. Lawrence Estuary and another in the Gulf part of the Laurentian channel towards the Cabot Strait. The boundaries of this specific benthic composition fitted almost exactly with the bathymetric morphology Laurentian channel but also with the Esquiman channel, where a similar community pattern is found. These particular assemblages can be qualified as "deep channel communities" (> 200 m). This group is characterized by the occurrence of organisms from Anthozoa taxa as individual contribution to similarities, such as Actiniaria and Pennatulacea (biomass and occurence databases). The SIMPER analysis also highlighted the presence of two species of echinoderm (*Ctenodiscus crispatus* and *Brisaster fragilis*) and an important contribution of *Syscenux infelix*. The heart urchin (*B. fragilis*) burrowing sand and mud substratum was often noticed with the deposit feeder *C. crispatus* (Whitford, 2007). Préfontaine and Brunel (1962) found matching distribution patterns for several of these most common species in the Gulf and the Estuary. According to the MDS plot (based on biomass data), a change in community's assemblages from the Lower Estuary to the Gulf was observed. Scyphozoa species and the occurrence of *Illex* sp. were noticed in the Gulf part of the Laurentian channel. A similar distribution of *Illex illecebrosus* was observed by Chabot *et al.* (2007)

with a higher concentration in the area of Cabot Strait. As it is suggested by Chabot *et al.* (2007), the distribution of *Illex* sp. was probably more influenced by the circulation conditions and presence of pelagic prey than by seabed parameters. Indeed, it was revealed by Dawe *et al.* (2000) that the abundance and distribution of short-finner squid could be influenced by the Gulf Stream dynamic. Besides, the northern edge of the Gulf Stream, is closed to the mouth of the Laurentian Channel (Gilbert *et al.*, 2005). Furthermore, it is interesting to notice the occurrence of the isopod, *S. infelix* and *Nezumia bairdii* at the same stations. Ross *et al.* (2001) proposed that the association of these two species was best described as obligate parasitism. It can partly explain this overlap of the geographic and bathymetric ranges.

Other assemblages where distinguished near Anticosti island (west, southwest and east parts) and also on the west coast of Newfoundland. These communities (Group VI in biomass data, Group II in occurence database) were characterized by the contribution of two anemone species: *Bolocera* sp. and *Hormathia nodosa*. The spatial distribution of these macrofauna communities corresponded to areas of high trawling intensity in the northern Gulf of St. Lawrence (Fig. 5b, in Kulka and Pitcher, 2001). As revealed by Jonsson *et al.* (2001), the anemone *Bolocera* sp is characterised as a voracious predator capturing plankton such as krill but also fish and shrimp, whereas the feeding type of *H. nodosa* consists of a variety of invertebrates and even small fishes (Jackson and Hiscock, 2004). These species can then feed on animals damaged by trawling operations, including discarded animals, which can explain the great contribution of these two species in these specific fishing areas (Kaiser and Spencer, 1996).

1.4.2 Spatial variability of benthic diversity

Significant differences were observed in the diversity among regions of the St. Lawrence system. A greater number of species was recorded at the head of the Laurentian channel stations, while a lower diversity value was recorded in the Middle Estuary. This is in contradiction with the Rapoport's rule which mentioned which diversity decreased from the ocean to upstream (Rapoport, 1994). This could be explaining by the depth differences observed between head and the mouth of the Gulf that is deeper. Bourque (2008) observed the same patterns with infaunal community for the area. According to Levin *et al.* (2001), the species richness is low at lowest food supply. This specific condition, insufficient resources to support populations of many species, was observed downstream the St. Lawrence Estuary (Desrosiers *et al.*, 2000) and could explain the pattern identified in the present study. A second explanation is the drastic changes in depth at the head of the Laurentian channel that generated a cold water upwelling associated with an important nutrient enrichment of the surface water (Therriault and Lacroix, 1976; Koutitonsky and Bugden, 1991). The intense mixing process observed delivers an important food supply for the macroepibenthic organisms. Moving from the Lower Estuary to the Gulf, the input of food supply in the Laurentian channel gradually decreases. Moreover, as it has been noted previously, Mingan Island vicinity and Strait of Belle-Isle were also characterized by the presence of specific hydrodynamic processes (Fuentes-Yaco, 1996; Le Fouest, 2005) bringing favorable conditions in food supply for macrobenthic species in these particular regions of the St. Lawrence system.

1.4.3 Biotic- abiotic interactions

Few studies have been conducted with the objectives of determining quantitatively the spatial variation and distribution of the macrobenthos in the St. Lawrence ecosystem, and finding the driving forces structuring these infaunal patterns (Desrosiers *et al.*, 2000; Bourque, 2008) or hard substratum benthic community (Ardisson and Bourget, 1992; Bourget *et al.*, 2003). In the present study, CCA highlight the importance of environmental factors in explaining the distribution of macrofaunal organisms. No single factor appeared to be a directing variable controlling benthic species distribution and richness in the St. Lawrence ecosystem. However, depth, temperature, bottom-water oxygen saturation, maximal bottom current and presence of pelite and gravel in the sediment composition, appear to be the important structuring forces on the invertebrate assemblages. The present results showed that the direction and the magnitude of temperature and depth were very similar whereas oxygen saturation was inversely correlated. It suggests that epibenthic macrofauna found at sampling stations with a pelite composition of substrata were also affected by the bottom current intensity and by temperature and depth parameters. On the other hand, the oxygen saturation level mostly influenced invertebrates at coarser substratum stations.

Canonical analysis indicated that temperature might affect the distribution of macrofaunal communities, especially on "deep channel community" (Group IV in Fig.8), as was also found in several benthic studies (Jennings *et al.*, 1999; Ellis *et al.*, 2000). However, the relationship in the present study of temperature with depth is expected to be

causal. The variation of those two parameters was very similar. As suggested by Ardisson *et al.* (1990), the inclusion of depth may limit the exploration of the variable likely to influence geographical variation of organism distribution. Nevertheless, temperature could influence the benthic invertebrate development rate (Peters, 1983; Miller and Emlet, 1999), spawning time (Himmelman, 1975) and the predator-prey control (Freitas *et al.*, 2007).

1.4.4 Influence of hypoxia

An oxygen gradient was observed from the head of the St. Lawrence channel to Cabot Strait, the bottom oxygen saturation being lower in the Estuary than in the Gulf (Gilbert *et al.*, 2005). In the canonical analysis, excluding the importance of the pelite and gravel sediment, dissolved oxygen (DO) in the bottom water appeared to be a driving factor of the distribution of epibenthic macrofaunal species in the Estuary and the northern Gulf of St. Lawrence. The presence of persistent hypoxic water in the Lower St. Lawrence Estuary (LSLE) was observed by Gilbert *et al.*, (2005). The oxygen levels recorded for bottom waters were less than 20% saturation (<60 μmol L^{-1}). Oxygen deficiency is a significant factor affecting the living conditions and the distribution of benthic fauna in deep waters (Laine *et al.*, 1997). Bourque (2008) observed that hypoxia condition can also affect the spatial distribution, diversity and feeding mode of benthic infauna organisms in the LSLE. Moreover, the bioturbation of the epibenthic fauna seems to be also influenced by the diminution of DO, with an increasing area covert by total and surface traces produced by the organisms (Belley *et al.*, 2008). However, the effect of

hypoxia differs among marine organisms. The literature shows that fishes are more vulnerable to reduced dissolved oxygen concentrations than many benthic organisms (Rosenberg *et al.*, 1992; Nilsson and Rosenberg, 1994). Nevertheless, within each taxa, variability was observed to be dependent on the habits of the species considered (Gray *et al.*, 2002). Recently, Vaquer-Sunyer and Duarte (2008) showed that crustaceans were more sensitive to hypoxia conditions (highest LC_{50}, shortest LT_{50}), whereas molluscs and cnidarians were more tolerant (lowest LC_{50}) to the same conditions. Accordingly, this specific spatial distribution pattern of those three taxa was also observed at hypoxic stations of the LSLE. The variation in oxygen thresholds among taxa revealed differences in the adaptation and in the strategy of benthic organisms to survive in low oxygen conditions. Shick (1976) mentioned that, at comparable temperatures, the mud star *C. crispatus* have a higher resistance to hypoxia than that of any echinoderm in the literature. In our study *C. crispatus* was the most abundant in the LSLE, where the lowest oxygen saturation value was recorded.

1.4.5 Predicting model

The habitat suitability (HS) model highlights the importance of the physical environment parameters in the determination and characterization of seabed macrofauna habitat of the St. Lawrence. Though, in different ways, the observed benthic species component and assemblages responded significantly to the diverse interacting physical gradients. Model selection involved the contribution of four environmental factors: depth, temperature, oxygen saturation and bottom current. The resultant equation describes how

benthic assemblages varied according to changes in each of environmental factors. The strongest features of the model of axis 1 are temperature and depth, whereas the habitat model was not able to distinguish the community structure corresponding to the second axis, and the substrata variable was rejected by the model to explain the pattern (Appendix 6).

Furthermore, substrata have been one of the most important environmental factors explaining spatial patterns of macrofauna in past studies (Thorson, 1971; Rhoads, 1976). The current study showed a correlation between composition of pelite and gravel with macrofauna assemblages, but the substratum factor seems to be concealed behind the other most significant environmental factors measured. A similar study carried out in the Southern North Sea has shown the importance of bedstress on benthic community distribution of this area (Vaz *et al.*, 2006). The estimated bed shear stress, used in the study was a function of the maximal predicted tidal current. As a result, particular benthic community with intermediate value in the model was correlated with high seabed shear stress data. In fact, this parameter reflects the friction pressure found on the seabed and then was often directly correlated with the sediment particle size. In our study, as suggested by Newell *et al.* (1998), benthic community composition is not controlled by the simple granulometric properties of the sediment nor by the bathymetric features. For example, particle mobility and the association of biological and chemical factors operating over the long term must also be taken into account. Moreover, trophic composition of soft-bottom communities can be significantly correlated with factors such

as sediment stability, water and organic content and microbial biomass of sediment (Maurer and Leathem, 1981; Gaston, 1987).

However, depth, temperature, oxygen saturation and bottom current were the most significant predictors obtained by the HS model, where the strongest feature is depth. Furthermore, in previous studies conducted in the Gulf of St. Lawrence, few of these environmental parameters were accepted as driving factors of benthic infaunal assemblages (Desrosiers *et al.*, 2000; Bourque, 2008). The biological assemblage patterns observed in the present study are consistent with the patchiness of environmental parameters: shallow and deep areas, high and low temperatures, and high and low oxygen saturation values.

An interesting point is that the majority of the marine invertebrates have a planktonic larvae phase and we know that there are many factors influencing the distribution of these such as the offshore transport (Bhaud, 2000), sea current and turbulence (Pedersen *et al*, 2007). In fact, we observed differences in community assemblages among the different zones of the study area, and we know that the environmental parameters were also spatially variable in the St. Lawrence. Then, this heterogeneity of environmental characteristics could have affected the community assemblages over time, and thus influenced benthic diversity as it was observed in a study on navigational buoys covering the same studied area as this one (Witman *et al.*, 2008).

The HS map for macrofauna epibenthic organisms shows good agreements with the mean survey species richness map, but the high diversity spot at the head of the Laurentian channel was not reported with a high potential value in the model. In fact, it is important to note that the model do not explain all community variations. About 40% of the variation was explained by the model equation. This is a great starting point to habitat characterization of macrobenthic communities. Explanatory variables retained by HS model were maybe less representative for this specific zone at the head of the Laurentian channel. Moreover, the model showed the occurrence of sub-communities, it is not about diversity or abundance. Nevertheless, the concordance with diversity map and HS model can confirm the presence of a potential biodiversity protected area.

Between 1990 and 2006 Chabot *et al.* (2007) proposed a preliminary division of the Estuary and Gulf of St. Lawrence (including the south part) about the benthic invertebrates collected during the different surveys in the same study area.This division contains 17 ecologically and biologically significant areas (EBSA) (Fig. 14, in Chabot *et al.*, 2007). Interestingly, close similarities were observed between the EBSA of Chabot *et al.* (2007) and high suitability zones of our predicting model, such as Jacques-Cartier strait, Mécatina Trough, Strait of Belle-Isle, St. George Bay, and Honguedo Strait on the southwestern part of Anticosti Island. However, the geographic coverage was different than the one in our study. Furthermore, the taxonomic resolution was not similar. In fact, invertebrates data used to delimit the EBSA were more accurate for shrimp and crab species and than for the other non-commercial invertebrate organisms. Indeed, data were mainly based from multispecific surveys conducted before the intensification of the

identification effort for all benthic invertebrate taxa. Chabot *et al.* (2007) study was more representative for commercial species while the prediction model of the current study was more robust for non-commercial benthic invertebrate species, the concordances found in both studies illustrated the potential relationships between shrimp species and other benthic invertebrate taxa collected at the same areas. As suggested by Fortin *et al.* (2005), many methods can be used to provide complementary and useful quantitative information for species occupancy range.

Nearly 40% of the variation in the macrofauna epibenthic communities was explained by the significant environmental variables: depth, temperature, bottom current and oxygen saturation. Thus, the environmental descriptors available in the present study can provide an acceptable prediction of macrofauna benthic habitat. As well as, the HS model predicts the occurrence of communities that have the possibility of colonizing each type of habitat. However, natural and anthropogenic impacts can change the macrobenthic community, resulting in the absence of predicted species or the presence of unexpected organisms. But to understand how such benthic assemblages may respond to disturbance, it is fundamental to first measure natural pattern of spatial difference and temporal change (Robert *et al.*, 2006). This research has successfully gathered a primary base of knowledge on the benthic habitat type and physical environment in the St. Lawrence system. As proposed by Engler *et al.* (2004), this kind of model could be used to predict locations of the most suitable (and unsuitable) habitats for species, communities or biodiversity.

1.5 Conclusion

In this first large-scale characterization of benthic macrofauna study, we used multivariate and geostatistical techniques, and then a mapping approach. Through the use of multivariate analyses, we defined eight biogeographic regions. The 200 m depth contours broadly defined benthic structure resulting in deep channels and shallower area communities. Hydrodynamic and physical conditions found in the St. Lawrence were also responsible for the main divisions between benthic communities (structure and diversity), especially coastal upwelling and presence of sill at specific areas. Moreover, macrofauna diversity, as well as community structure, was closely correlated with the presence of these major structures in the circulation pattern. Indeed, the head of the Laurentian channel, Mingan Island vicinity, and Strait of Belle-Isle were characterized by upwelling, tidal mixing and presence of sill, resulting in higher diversity spots.

The water depth, bottom temperature, oxygen saturation, maximal bottom current and presence of pelite and gravel in the sediment were the main explanatory variables for the distribution of the benthic community, highlighted by the canonical analyses. These analyses were used to reflect the ecological preferences of the macrofauna communities and particular species colonizing the available habitat. A well-defined difference in epibenthic faunal association, was exposed in the canonical graphs, in two specific habitat types: (1) deeper stations are mostly composed of fine substrata (pelite) and higher temperature, mainly composed of Actiniaria species, *C. crispatus* and *B. fragilis*, and; (2) shallower stations with presence of coarser sediment type and higher oxygen

saturation level are characterized by the presence of *Strongylocentrotus* sp., *Henricia* sp., and *Ophiopholis aculeata*. As expected, epibenthic organisms were influenced by the low oxygen concentration in the LSLE. The lower density of crustaceans at hypoxic stations underlines the vulnerability of these species compared with tolerant organisms, such as cnidarians and molluscs. Potential impact of long term hypoxia phenomenon in the LSLE needs to better understand.

The predicting habitat suitability model accepted all the same significant environmental variables than canonical analyses, excluding sediment type.

Axis 1 ~ oxygensaturation^2 + depth + depth^2 + temperature + temperature^2 + bottomcurrent^2

Our study clearly demonstrated the usefulness of bottom trawl observations, during fisheries survey, to infer the relationships of benthic macrofauna community structure and environmental variables. This predicted habitat suitability map is simply a preliminary basis to which further physical and chemical parameters should be added in order to bring the description of this habitat closer to reality. In the future, modelling could be used to improve our understanding about key and indicator species distribution or to indicate potential hotspot area of benthic organisms. This model will be very useful to monitor spatially and temporally the quality of these benthic habitat types and then should help elaborating conservation and protection strategies to reduce impacts of natural or anthropogenic disturbances.

CONCLUSION GÉNÉRALE

Un relevé estival multidiciplinaire de chalutage de fond du ministère des Pêches et Océans Canada (région du Québec) est réalisé annuellement dans le nord du Golfe du Saint-Laurent. Un des objectifs principaux de ce relevé est de dresser le bilan global pour les stocks des principales espèces commerciales. En août 2006, ce relevé a servi pour la première fois de banc d'essai pour la collecte de données sur l'ensemble de la faune d'invertébrés benthiques (commerciale et non-commerciale). Étant donné les caractéristiques du chalut de fond (chalut à crevettes *Campelen 1800*) utilisé lors de ce relevé, la macrofaune benthique échantillonnée pour cette étude est majoritairement composée d'organismes épibenthiques, sans toutefois s'y limiter. Ainsi, la présence de quelques espèces bentho-pélagiques est également observée. Bien que la benne soit reconnue comme un outil d'échantillonnage beaucoup plus précis pour des études quantitatives sur la faune benthique, l'utilisation de cet engin crée des contraintes en temps d'opération qui peuvent s'avérer onéreuses lorsqu'il s'agit d'évaluer un aussi grand territoire (plus de 115 000 km^2) que celui couvert par le relevé. De plus, l'échelle examinée dans cette étude, qui est de décrire l'habitat des différentes espèces épibenthiques est beaucoup plus grande que l'échelle ponctuelle couverte par la surface échantillonnée d'une benne (Callaway *et al.,* 2002). D'où l'avantage d'utiliser le chalut dans la présente étude qui a entre autre comme objectif de recueillir de l'information sur les habitats potentiels de la faune benthique.

Dans le même ordre d'idée, des données sur l'efficacité de l'engin de pêche au niveau de l'échantillonnage des invertébrés démontrent que l'utilisation du nouveau chalut à crevettes à quatre faces, de type *Campelen 1800*, a un rendement nettement meilleur que le chalut à crevettes *URI 81'/114'* utilisé de 1990 à 2003 au cours de ce relevé estival. De fait, au niveau de l'Estuaire, les données montrent qu'avant 2003, environ 80% de la biomasse totale des invertébrés capturés était composée de crevette nordique, contre seulement 20% de l'ensemble de la biomasse totale regroupant tous les autres taxa d'invertébrés répertoriés. Tandis que depuis l'utilisation du nouveau chalut (depuis 2005), la biomasse totale de toutes les autres espèces d'invertébrés était alors estimée à près de 72% de la biomasse totale d'invertébrés capturés (C. Savenkoff, comm. pers.). De tels résultats illustrent bien l'efficacité du chalut de type *Campelen 1800* utilisé à titre d'outil d'échantillonnage des communautés benthiques visées. Tout en étant conscient que l'engin de pêche ici utilisé ne représentait pas une précision maximale d'échantillonnage, il demeurait tout de même pertinent pour une étude de caractérisation du milieu à grande échelle. De plus, il est important de noter que, pour l'ensemble de la zone d'étude, les données d'abondance ont été standardisées en fonction de la surface chalutée et du temps de pêche réalisé à chaque station.

Cette étude se veut essentiellement être une étude de caractérisation du milieu en dressant une image globale de la distribution à grande échelle de la macrofaune benthique de l'Estuaire et du nord du Golfe du Saint-Laurent. L'approche utilisée, jumelant les analyses multivariées et les techniques de géostatistiques, a permis de recueillir un bagage important de connaissances sur la distribution spatiale des communautés

benthiques et des variables environnementales du milieu qui agissent à titre de forces structurantes sur ces organismes. Cette étude a tout d'abord permis de confirmer et de préciser les divisions biogéographiques des communautés benthiques du Golfe, antérieurement établies par Brunel *et al.* (1998). En outre, les unités de production du crabe des neiges, identifiées par Sainte-Marie *et al.* (2005), ont également été considérées pour clarifier certaines zones. La division en huit assemblages distincts semble être reliée aux caractéristiques hydrodynamiques (upwelling, rencontre de masse d'eaux, présence de seuil) et topographiques du milieu (bathymétrie), tel que mentionné dans la littérature portant sur le sujet (Koutistonsky et Bugden, 1991; Brunel *et al.*, 1998 ; Bourget *et al.*, 2003 ; Sainte-Marie *et al.*, 2005). Ces caractéristiques océanographiques distinctes observées dans les différentes subdivisions biogéographiques de la zone d'étude semblent également influencer la diversité se rapportant au nombre total d'espèces par station. À titre d'exemple, les zones à plus forte diversité benthique telles que la région de la Minganie et du détroit de Belle-Isle, concordent parfaitement bien avec les subdivisions reconnues dans la littérature au niveau de ces régions.

Selon différents auteurs, une variété de paramètres environnementaux peuvent agir de concert sur la composition spécifique (Freeman et Rogers, 2003). Globalement, dans la présente étude, la profondeur, la température, l'oxygène dissout, les courants de fond et la présence de pelite et de gravier dans les sédiments, ont été les paramètres environnementaux retenus comme variables significatives par les analyses canoniques en tant que force structurante.

Dans le même ordre d'idée, une étude portant sur la variabilité spatio-temporelle de l'endofaune du Saint-Laurent a également révélé l'influence significative de la température sur la répartition spatiale de ces communautés d'invertébrés benthiques, tout comme sur leur diversité et leurs modes d'alimentation (Bourque, 2008). De plus, l'oxygène dissout présent dans les fonds du Saint-Laurent a également été reconnu comme un facteur principal pouvant expliquer la répartition et le comportement des organismes épibenthiques. Une étude en cours de réalisation expose d'ailleurs l'importance de la diminution de l'oxygène dissout sur la présence et le type de traces de bioturbation laissées par la faune benthique (Belley *et al.*, 2008). Par contre, il est important de noter que les résultats actuels de la répartition des organismes au niveau de la zone qualifiée hypoxique en 2003, semblent contredire les conclusions de travaux antérieurs qui présentaient les conséquences de l'hypoxie sur la faune benthique (Diaz et Rosenberg, 1995; Wu, 2002). Cela pourrait en fait indiquer que cette zone précise de l'Estuaire maritime du Saint-Laurent est présentement en état de transition (Belley *et al.*, 2008). Déjà un changement dans la structure des communautés benthiques est observé. On y note entre autre une augmentation des déposivores qui sont des organismes plus tolérants à un faible taux d'oxygène dissout (Bourque, 2008). Par conséquent si la diminution de l'oxygène perdure dans l'EGSL, tout porte à croire que les observations sur la diversité benthique, ainsi qu'au niveau des traces de bioturbation laissées par les organismes, tendront alors vers les mêmes tendances que celles observées dans la littérature sur le sujet.

Finalement, un modèle linéaire généralisé (GLM) a été utilisé afin de prédire les habitats potentiels des communautés benthiques en fonction des paramètres environnementaux disponibles. La modélisation a par contre exclu la variable « substrat » des paramètres environnementaux retenus par les analyses canoniques. L'équation finale de l'axe 1 du modèle de prédiction établi qui tenait compte de la profondeur, de l'oxygène dissout, de la température et des courants de fond, permet d'expliquer à près de 40 % la variation des communautés benthiques dans la zone d'étude. Le modèle de l'axe 2 qui intégrait la variable substrat, a dû quant à lui être rejeté étant donné que la majorité des variables ont été identifiées comme non significatives. Par contre, les résultats de ce second modèle, ainsi que ceux des analyses canoniques, portent à croire que la variable substrat a un rôle à jouer dans la structure des communautés. Toutefois, cette unique information concernant le type de substrat ne peut être considérée comme étant un paramètre structurant significatif qui agit sur les communautés d'invertébrés benthiques.

Ainsi au cours des prochaines années, il serait souhaitable de porter une attention particulière quant aux caractéristiques intrinsèques des sédiments de fond telles que la taille moyenne des grains et le contenu en matière organique plutôt que la nature même du substrat, afin d'améliorer le modèle. Le modèle de prédiction de l'axe 1 qui intègre les variables courant et profondeur, incopore peut-être la composante substrat puisque la taille des sédiments de fond est reconnue pour être effectivement influencée par le « bedstress » (Vaz *et al.*, 2006).

De plus, les paramètres d'hétérogénéité et de topographie du fond pourraient également être considérés à titre de facteurs influant sur la distribution des communautés benthiques (Archambault et Bourget, 1996; Newell *et al.*, 1998). Qui plus est, les analyses n'ont pas retenu la concentration en chlorophylle *a* comme une variable significative et ce, bien que bon nombre d'études en mentionnent l'importance sur la faune benthique (Hobson *et al.*, 1995; Piepenburg, 2005; Feder *et al.*, 2007). Il serait donc approprié, lors des études ultérieures, d'utiliser des moyennes annuelles ou mensuelles de cartes continues obtenues à partir d'observations satellitaires, plutôt que des valeurs ponctuelles enregistrées lors de l'échantillonnage effectué à bord du navire.

Les zones de fond affectées par les opérations de chalutage pratiquées par la pêche commerciale, de même que l'intensité de perturbation (fréquence de chalutage), sont autant d'éléments qui seraient intéressants d'intégrer dans la procédure de modélisation. En effet, le phénomène de la diminution de la ressource (diversité, productivité et abondance des espèces) est très souvent soulevé dans les études sur les pêches et demeure un enjeu de taille. Dans cette optique, plusieurs recherches ont étudié les impacts potentiels des engins de pêche sur les habitats benthiques (Kaiser et Spencer, 1995 ; Turner *et al.*, 1999 ; Thrush et Dayton., 2002). Tel que mentionné par Pitcher (2001), les espoirs de protéger la ressource s'appuient sur l'orientation des mesures de conservation qui doivent être davantage axées sur la reconstruction de l'écosystème global, plutôt que sur une espèce précise. D'où l'importance indéniable de tenir compte de la faune benthique et d'améliorer nos connaissances sur ces communautés.

Par ailleurs, l'indice de diversité utilisé dans la présente étude, soit le nombre d'espèces retrouvées sur une surface de chalutage donnée (par station), n'est pas la mesure la plus robuste qui soit. Cet indice peut en effet être influencé par la taille de l'échantillon. Ainsi une surface d'échantillonnage plus grande devrait contenir un plus grand nombre d'espèces. Il aurait donc été préférable d'utiliser un indice de diversité qui soit indépendant de la surface d'échantillonnage telle que l'indice de raréfaction de Hurlbert (1971), ES_x. L'idée étant de générer une mesure absolue de la richesse spécifique sur un échantillon de taille déterminée, comme par exemple pour un groupe de 50 individus (ES_{50}). Par contre dans le contexte actuel, cet indice n'était pas applicable puisque nous avions deux bases de données distinctes sous deux unitées différentes. Utlérieurement il serait donc intéressant d'approfondir cet aspect de l'analyse des résultats afin d'obtenir une autre mesure de la diversité retrouvée à chacune des stations. Permettant ainsi de confirmer ou infirmer les données actuelles de la distribution de la richesse spécifique sur le territoire à l'étude (nombre d'espèce par station).

Cette étude démontre bien la pertinence de l'approche de modélisation d'habitat, associée aux techniques de géostatistiques et de cartographie ArcGIS. Pour le futur, de tels outils apparaissent essentiels pour la gestion durable et la protection des ressources afin, entre autres, de mettre en évidence des zones de grande biodiversité (« hotspot ») ou encore afin de déterminer les habitats pour les espèces indicatrices ou menacées. Il serait également intéressant de voir la possibilité d'utiliser ces méthodes dans un contexte de réchauffement climatique et ainsi tenter de prédire les impacts potentiels de l'augmentation de la température sur la structure des communautés benthiques. Une telle

analyse a d'ailleurs été appliquée au niveau de la Manche Orientale par les scientifiques de l'IFREMER (Boulogne-sur-mer) (Vaz *et al.*, 2008).

Un dernier point important à mentionner est la prise en compte de la variabilité intrinsèque (biotique) des communautés. Bon nombre de travaux de Guichard (2003, 2005, 2008), défendent l'idée de vérifier l'importance de ce paramètre (à grande échelle) identifié dans un milieu environnemental très hétérogène. Globalement, il s'agit d'étudier à quelles échelles les processus biologiques telles que les distances de dispersion et de compétition interagissent avec l'environnement à titre de mécanisme structurant spatial (Snyder et Chesson, 2004). Une validation de cette hypothèse pourrait s'avérer pertinente et révélatrice.

Pour conclure, l'ensemble des informations obtenues à partir de ce relevé de chalutage de fond pourra fournir aux collectivités un outil d'aide décisionnel pour les gestionnaires en dressant une image plus concrète et intégrée du monde marin. La clé de la réussite pour une gestion durable et la protection des ressources réside dans la mise en commun des connaissances de l'ensemble des intervenants concernés.

Puisque pour protéger l'environnement, il faut d'abord apprendre à le connaître.

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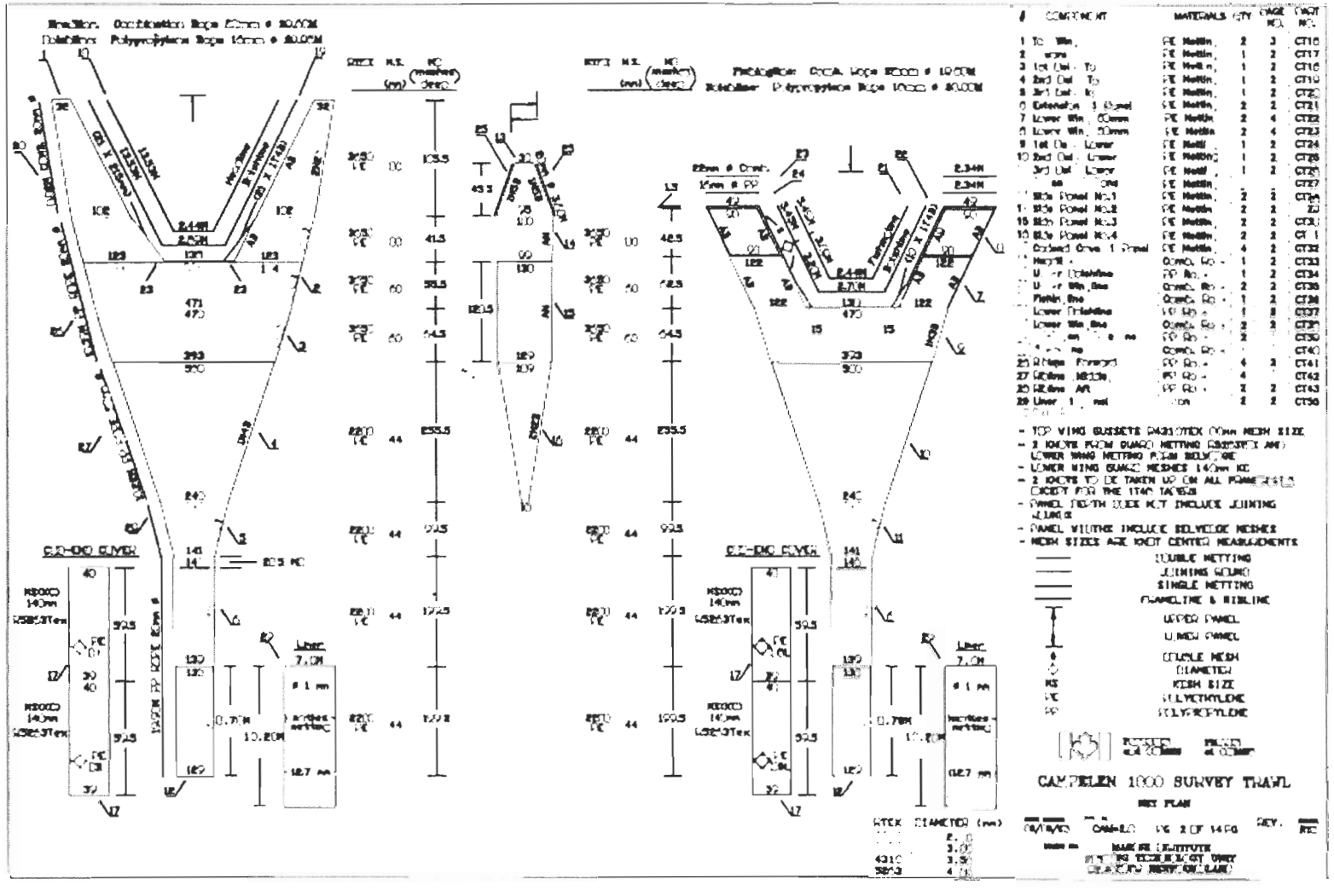
ANNEXES

Annexe 1. Schéma du chalut à crevette à quatre faces de type *Campelen 1800*, utilisé sur le NGCC *Teleost* (tiré de McCallum et Walsh, 1997)



Annexe 2. Liste des taxons de la macrofaune épibenthique répertoriés dans l'Estuaire et le nord du Golfe du Saint-Laurent en 2006

Phylum	Classe	Ordre	Famille	Espèce
Annelida	Polychaeta	Aciculata	Aphroditidae	*Aphrodita hastata*
				Laetmonice filicornis
			Lumbrineridae	*Lumbrineris fragilis*
			Nepthtyidae	*Nepthys bucera*
				Nepthys discors
			Onuphidae	*Onuphis opalina*
			Sillidae	*Sillides setosa*
				Ondotosyllis fulgurans
		Canalipalpata	Terebellidae	*Neoamphitrite affinis*
			Pectinariidae	*Pectinaria granulata*
			Serpulidae	*Spirorbis* sp
				Spirobis spirorbis
		Capitallida	Nereididae	*Nereis pelagica*
			Polynoidae	*Harmothoe* sp.
				Harmothoe extenuata
				Harmothoe nodosa
				Harmothoe oerstedi
				Harmothoe spinosa
				Enipo torelli
			Scalibregmatidae	*Scalibregma inflatum*

Phylum	Classe	Ordre	Famille	Espèce
Arthropoda	Malacostraca	Isopoda	Aegidae	*Aega psora*
				Syscenus infelix
		Amphipoda	Epimeriidae	*Epimeria loricata*
				Paramphitoe hystrix
			Eusiridae	*Eusirus cuspidatus*
				Rhachotropis aculaeta
			Hyperiidae	*Themisto libellula*
			Stegocephalidae	*Stegocephalus inflatus*
			Uristidae	*Anonyx* sp.
		Sessilia	Archaeobalanidae	*Chirona hameri*
				Semibalanus sp.
			Balanidae	*Balanus balanus*
				Balanus crenatus
	Maxillopoda	Pedunculata	Scalpellidae	*Arcoscalpellum michelottianum*
		Decapoda	Paguridae	*Pagurus* sp.
				Pagurus arcuatus
				Pagurus pubescens
			Galatheidae	*Munidopsis curvirostra*
		Calanoida	Calanidae	*Calanus finmarchicus*

Phylum	Classe	Ordre	Famille	Espèce
Arthropoda	Pycnogonida	Pantopoda	Nymphonidae	*Nymphon* sp.
				Nymphon grossipes
				Nymphon macrum
				Nymphon stroemi
Chordata	Ascidiacea	Enterogona	Cionidae	*Ciona intestinalis*
		Pleurogona	Pyuridae	*Boltenia ovifera*
				Boltenia echinata
				Halocynthia pyriformis
			Molgulidae	*Molgula citrina*
				Molgula complanata
				Molgula tubifera
Cnidaria	Anthozoa	Actiniaria	Actiniidae	
				Bolocera sp.
			Actinostolidae	*Stomphia coccinea*
			Hormathiidae	*Hormathia nodosa*
				Stephanauge nexilis
		Alcyonacea	Alcyoniidae	*Duva* sp.
				Gersemia sp.
Cnidaria	Anthozoa	Scleractinia	Flabellidae	*Flabellum* sp.
		Pennatulacea	Pennatulidae	*Pennatula* sp.

Phylum	Classe	Ordre	Famille	Espèce
Cnidaria	Hydrozoa	Leptothecatae	Campanulariidae	*Campanularia* sp.
			Lafoeidae	*Lafoea* sp.
				Lafoea fructicosa
			Sertulariidae	*Abietinaria abietina*
				Sertularella polyzonias
				Sertularia fabricii
				Thuiaria sp.
				Thuiaria thuja
				Thuiaria articulata
				Thuiaria distans
			Haleciidae	*Halecium beanii*
			Laodiceidae	*Ptychogena lactea*
		Anthoathecatae	Stylasteridae	*Crypthelia affinis*
	Scyphozoa			
Echinodermata	Asteroidea	Forcipulatida	Asteriidae	*Asterias rubens*
				Leptasterias polaris
				Leptasterias littoralis
				Stephanasterias albula
		Spinulosida	Asterinidae	*Tremaster mirabilis*
			Echinasteridae	*Henricia* sp.
			Poraniidae	*Poraniomorpha hispida*
			Pterasteridae	*Pteraster affinis*
				Pteraster militaris

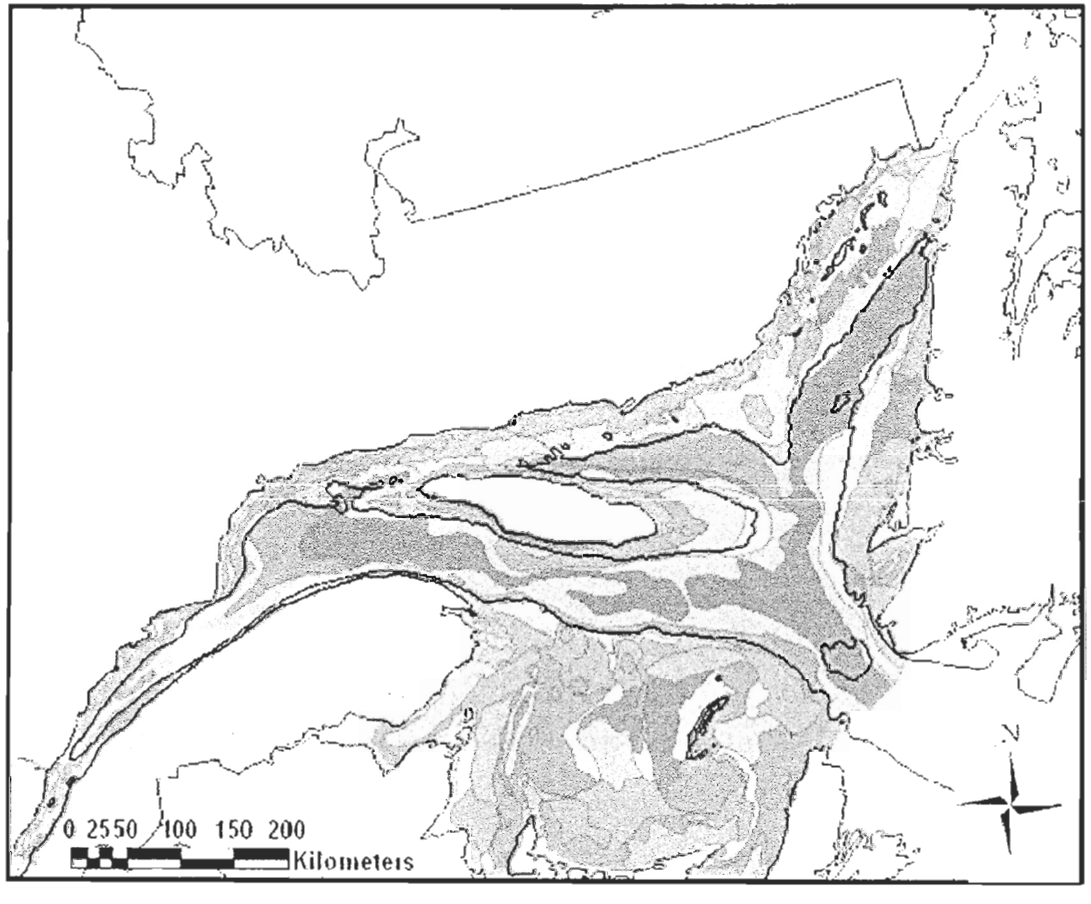
Phylum	Classe	Ordre	Famille	Espèce
Echinodermata	Asteroidea	Spinulosida	Solasteridae	*Crossaster papposus*
				Solaster endeca
		Paxillosida	Astropectinidae	*Leptychaster arcticus*
				Psilaster andromeda
				Plutonaster agassizi
			Goniopectinidae	*Ctenodiscus crispatus*
		Valvatida	Goniasteridae	*Ceramaster granularis*
				Hippasteria phrygiana
				Pseudarchaster parelii
	Holothuroidea	Dendrochirotida	Cucumariidae	*Cucumaria frondosa*
			Psolidae	*Psolus fabricii*
				Psolus panthapus
		Molpadiida	Molpadiidae	
	Ophiuroidea	Phrynophiurida	Gorgonocephalidae	*Gorgonocephalus arcticus*
		Ophiurida	Ophiactidae	*Ophiopholis aculeata*
			Ophiocanthidae	*Ophiacantha bidentata*
			Ophiuridae	*Ophiura sarsi*
				Ophiura robusta
		Phrynophiurida	Ophiomyxidae	*Ophioscolex glacialis*
	Echinoidea	Spantagoida	Schizasteridae	*Brisaster fragilis*
		Echinoida	Strongylocentrotidae	*Strongylocentrotus* sp.
		Clypeasteroida	Echinarachiidae	*Echinarachnius parma*
	Crinoidea	Comatulida	Antedonidae	*Antedon bifida*

Phylum	Classe	Ordre	Famille	Espèce
Ectoprocta	Articulata	Terebratulida	Cancellothyrididae	*Terebratulina septentrionalis*
		Rhynchonellacea	Hemithyrididae	*Hemithiris psittacea*
	Gymnolaemata	Cheilostomata	Scrupocellariidae	*Caberea ellisii*
			Stomachestosellidae	*Posterula sarsi*
Mollusca	Bivalvia	Veneroida	Astartidae	*Astarte* sp.
				Astarte crenata subequilatera
				Astarte castanea
				Astarte borealis
				Astarte montagui
				Astarte undata
			Cardiidae	*Clinocardium ciliatum*
			Carditidae	*Cyclocardia borealis*
			Mesodesmatidae	*Mesodesma deauratum*
			Tellinidae	*Macoma* sp.
		Arcoida	Arcidae	*Bathyarca pectunculoides*
		Myoida	Hiatellidae	*Hiatella arctica*
			Myidae	*Mya truncata*
		Mytiloida	Mytilidae	*Mytilus edulis*
				Musculus niger
		Nuculoida	Nuculidae	*Nucula* sp.
			Yoldiidae	*Megayoldia thraciaeformis*
				Yoldia myalis
		Ostreoida	Pectinidae	*Chlamys islandica*
				Placopecten magellanicus
				Delectopecten vitreus

Phylum	Classe	Ordre	Famille	Espèce
Mollusca	Bivalvia	Pholadomyoida	Cuspidariidae	*Cuspidaria glacialis*
	Gastropoda	Neogastropoda	Buccinidae	*Buccinum* sp.
				Buccinum plectrum
				Buccinum totteni
				Buccinum undatum
				Plicifusus cretaceus
				Colus sp.
				Colus pubescens
				Colus stimpsoni
				Colus pygmaeus
				Neptunea sp
				Neptunea lyrata decemcostata
				Neptunea brevicauda
		Archaegastropoda	Trochidae	*Solariella obscura*
		Cephalaspidea	Cylichnidae	*Scaphander* sp.
		Neogastropoda	Muricidae	*Boreotrophon clathratus*
				Boreotrophon truncatus
		Archaeogastropoda	Calliostomatidae	*Calliostoma occidentale*
			Trochidae	*Margarites* sp.
				Margarites costalis
				Margarites groenlandicus

Phylum	Classe	Ordre	Famille	Espèce
Mollusca	Gastropoda	Nudibranchia	Chromodorididae	*Cadlina laevis*
			Polyceridae	*Palio dubia*
			Dendronotidae	*Dendronotus frondosus*
		Cephalaspidea	Haminoeidae	*Haminoe solitaria*
		Neotaenioglossa	Naticidae	*Euspira pallida*
				Polinices heros
				Polinices immaculatus
			Velutinidae	*Velutina undata*
			Aporrhaididae	*Aporrhais occidentalis*
			Turritellidae	*Turritella aigue*
	Polyplacophora	Neoloricata	Ischnochitonidae	*Tonicella rubra*
Mollusca	Cephalopoda	Octopoda	Octopodidae	*Bathypolypus* sp.
		Sepiolida	Sepiolidae	*Semirossia* sp.
Porifera				
Sipuncula			Golfingiidae	*Golfingia* sp.
				Golfingia margaritacea
			Phascolosomatidae	*Phascolosoma* sp.
Nemertea				

Annexe 3a. Carte de la distribution continue du sédiment de fond du Saint-Laurent (tirée de Loring et Nota, 1973)



Annexe 3b. Légende décrivant les types de sédiment de fond, utilisés pour les analyses

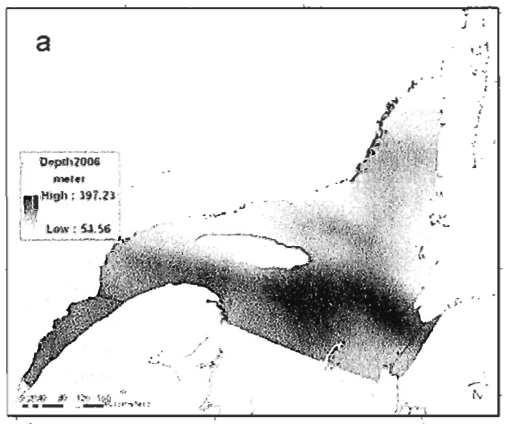
Pélite gravelo-sableuse; Pélite sableuse
Apports glaciaires brun-rougeâtre
Calcarénite
Calcarénite; Gravier avec des parcelles de sable occasionnelles
Calcarénite; calcirudite
Calcarénite; calcirudite; Sable gravelo-pélitique principalement retravaillé
Calcirudite
Calcirudite; calcarénite
Débris coquilliers
Gravier avec des parcelles de sable occasionnelles
Gravier avec des parcelles de sable occasionnelles; Gravier sableux
Gravier avec des parcelles de sable occasionnelles; Sable gravelo-pélitique principalement retravaillé
Gravier sableux
Gravier sableux; Sable gravelo-pélitique principalement retravaillé
Pélite
Pélite calcaire
Pélite graveleuse
Pélite gravelo-sableuse
Pélite résiduelle
Pélite sableuse
Pélite sableuse; Pélite gravelo-sableuse
Pélite sableuse; Sable pélitique mal trié
Pélite très sableuse
Pélite très sableuse; Pélite gravelo-sableuse
Sable fin argileux
Sable fin graveleux
Sable graveleux bien trié
Sable graveleux bien trié; Sable graveleux bien trié; Gravier avec des parcelles de sable occasionnelles
Sable graveleux bien trié; Sable gravelo-pélitique principalement retravaillé
Sable graveleux bien trié; Sable à grains moyennement grossier
Sable graveleux mal trié
Sable graveleux mal trié; Gravier avec des parcelles de sable occasionnelles
Sable gravelo-pélitique principalement retravaillé
Sable gravelo-pélitique principalement retravaillé; Gravier sableux
Sable gravelo-pélitique principalement retravaillé; Sable graveleux bien trié
Sable gravelo-pélitique principalement retravaillé; Sable graveleux mal trié
Sable gravelo-pélitique principalement retravaillé; Sable pélitique mal trié
Sable gravelo-pélitique principalement retravaillé; calcirudite
Sable pélitique mal trié
Sable pélitique mal trié; Sable gravelo-pélitique principalement retravaillé
Sable trié à bien trié
Sable trié à bien trié; Sable fin graveleux
Sable très fin
Sable à grains moyennement grossier
Sable à grains moyennement grossier; Sable graveleux bien trié
Sable à grains moyennement grossier; Sable graveleux mal trié

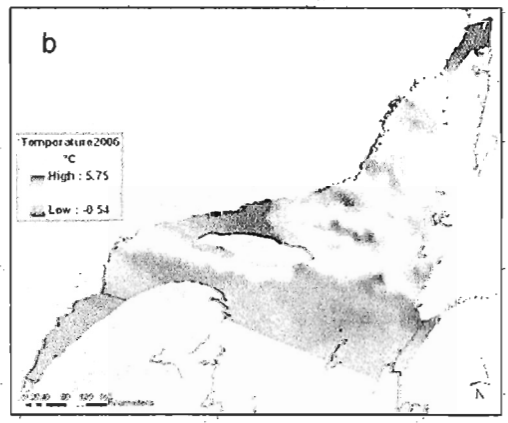
Annexe 4. Résultats des analyses de géostatistiques

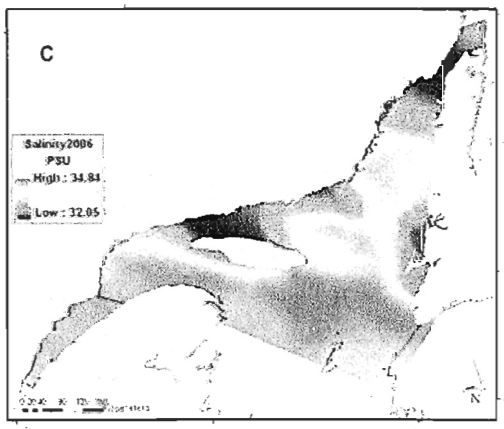
Variable environnementale	MODÈLE	Correspondance avec le modèle (%)
Courant maximal	Exponentiel	91
Oxygène	Exponentiel	96.6
Salinité	Exponentiel	100
Profondeur	Circulaire	97.5
Température	Shérique	98.5
Chlorophylle *a**	Exponentiel	99.7

* Un détendançage à été effectué sur les données de la chlorophylle *a*, ainsi ce sont les résidus de la régression quadratique qui ont été utilisés pour les analyses de géostatistique sur cette variable

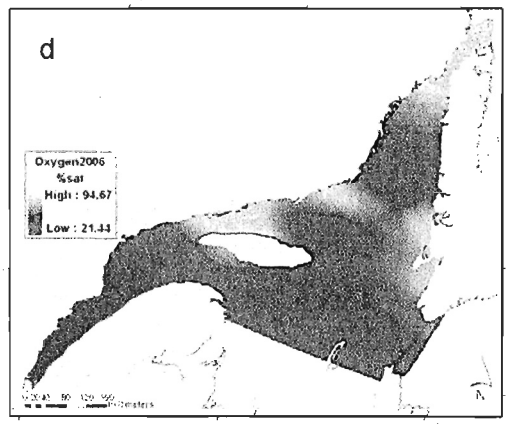
Annexe 5 a. Cartes de la distribution continue des variables environnementales étudiées : a) profondeur (m); b) température (°C); c) salinité (PSU)

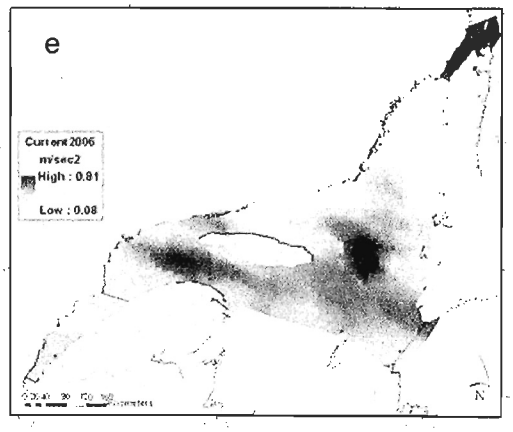


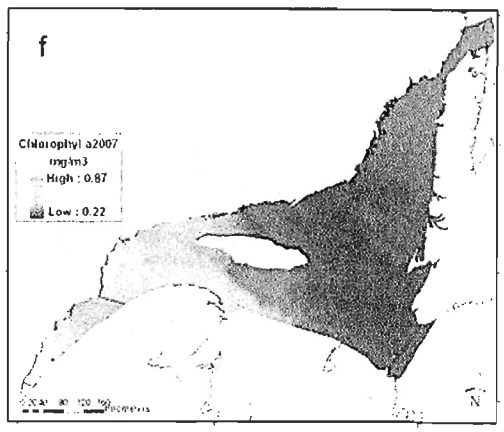




Annexe 5 b. Cartes de la distribution continue des variables environnementales étudiées d) oxygène dissous (% saturation); e) courant maximal de fond (m/s2); f) concentration chl a (mg/m3).







Annexe 6. Résultats de la validation du modèle linéaire généralisé (logiciel R).

	Axis 1			Axis 2		
	Coefficient	Spearman corr	Significatif code	Coefficient	Spearman corr	Significatif code
(Intercept)	4.73	0.00	***	-5.38	0.00613	**
oxygen saturation				0.14	0.00089	***
oxygen saturation2	0.00	0.03	*	0.00	0.05263	.
depth	-0.02	0.00	***	0.01	0.18351	
depth2	0.00	0.01	**	0.00	0.21479	
temperature	-0.85	0.00	***	0.63	0.05284	.
temperature2	0.09	0.00	**	-0.05	0.23131	
bottom current				-6.05	0.09974	.
bottom current2	1.42	0.02	*	9.38	0.05582	.
chlorophyll				-0.16	0.05573	.
chlorophyll2				0.01	0.12842	
Gdc sediment				-2.12	0.14777	
Ggs sediment				-1.04	0.32065	
Pp sediment				-1.63	0.06467	.
Ppc sediment				-1.02	0.25265	
Ppgs sediment				-1.03	0.23821	
Pps sediment				-0.59	0.47359	
Ppts sediment				-1.19	0.18279	
Pptspgs sediment				-1.13	0.21784	
SGcc sediment				-0.09	0.9178	
Ssfa sediment				0.13	0.89329	
Ssgmt sediment				-0.56	0.59885	
Ssgppr sediment				-0.24	0.7668	
Sspmt sediment				-2.22	0.09372	.